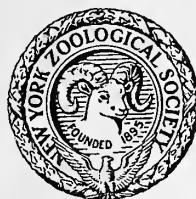


ZOOLOGICA

SCIENTIFIC CONTRIBUTIONS OF THE
NEW YORK ZOOLOGICAL SOCIETY

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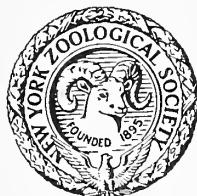
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Aspects of Melanism in Acanthopterygian Fishes

C. M. BREDER, JR.*

(Plate I; Text-figures 1-6)

Teleost fishes may show a strong melanism against a light background. This condition is found chiefly in young fishes of the families Carangidae, Sapridae, Sciaenidae, and Ephippidae during the warm half of the year. Social attitudes and locomotor behavior change with this darkening, including a solitary, quiescent, and agonistic attitude. This behavior mitigates the conspicuousness of this black phase, which has evidently been induced by former residence on a very dark background. This may return quickly to a light phase or be retained for a period of some weeks because of certain interactions within the neuro-endocrine system which control the pigment cells responsible for this phenomenon. The size at which fishes outgrow is related to the light intensity and water turbidity.

INTRODUCTION

IT HAS BEEN adequately shown that some species of acanthopterygians may be found in an intensely black condition although living over an extremely light background (Breder, 1946, 1948, 1949a, 1955, and 1959; and Breder and Rasquin, 1950 and 1955). This blackening is brought about by the usual piscine mechanism of pigment control, first by dispersion of the melanin granules contained within the melanophores, followed by the development of additional melanophores, leading to melanism. In this dark phase these fishes are solitary and quiet, usually "freezing" on approach, while in the lighter phases they are gregarious, active, and flee on approach. The situations which lead to the observed consequences are analyzed herein.

Help in collecting the information contained herein has come from many quarters and is chiefly noted in context. Special mention is given here, however, for the great assistance rendered by Dr. Eugenie Clark and her daughter, Hera Konstantinu. Both undertook considerable field work, and in addition Dr. Clark supplied many details of the area with which she is intimately familiar. Mr. Louis Godey, an NSF

summer student at the Cape Haze Laboratory, working under the direction of Dr. Clark, obtained valuable statistical and other data during the 1962 season in the Sarasota area. The Cape Haze Marine Laboratory (the Mote Marine Laboratory since 1967) provided needed facilities for the prosecution of this study. These facilities have been continued through the courtesy of the present director, Dr. Perry Gilbert.

The fine efforts of Miss Sarah L. Page, working with the author as a Lincoln Ellsworth Field Assistant, of the American Museum of Natural History, went far toward filling in needed information.

The work was supported in part by a grant (NSF-G-19382) from the National Science Foundation. Otherwise support was provided by the American Museum of Natural History.

THE NATURAL OCCURRENCE OF MELANISTIC INDIVIDUALS

Because of the general sensitivity of fishes to the shade and color of their backgrounds, presumably all teleosts with dermal or epidermal melanophores have the potential to darken their colors in response to a dark background. However some species cannot, or do not, do so to any noticeable extent and many can carry the condition only to a point far short of becoming black. Some cave fishes, but not all, have evidently lost their ability to produce melanophores, even when exposed to light. At least

* The American Museum of Natural History, New York, New York 10024, and Mote Marine Laboratory, Sarasota, Florida 33581.

certain of them do not produce melanophores, even though kept in light for generations (Breder and Rasquin, 1947, and Rasquin and Rosenbloom, 1954).

At the other extreme, various deep sea fishes have a more completely developed melanism than any others. These too are living in darkness, except that a vast variety of luminous invertebrates and melanistic fishes prevent the ocean abysses from being totally lightless. Significantly many of these forms, unlike the blind fish of fresh water caves, have not lost their eyes. No luminous aquatic creatures have been yet discovered in subterranean fresh waters. These conditions have usually been considered as basic to the extreme pigmentary differences between cave and abyssal fishes.

By contrast there are few epigean fishes, in either fresh or salt water, that are either pigmentless or completely black. So far as known, these few are all generally able to adjust their pigments, when appropriately stimulated, to patterns more usual in surface waters. The hypogean forms, marine or fresh water, apparently lack this ability to any considerable degree, as indicated above, and are thereby confined to a single pigmentary appearance.

The following accounts of field observations are limited to fishes that can show a completely or almost completely black aspect, in places subject to natural illumination, and in which they appear as solitary individuals. Black fish which appear in lighted environments only in aggregations are not included. Data and references to these may be found in Breder (1959) and Randall and Randall (1960).

Because of the nature of field notes, some part of the following matter is fragmentary and anecdotal, but in most instances represents all the existing information. These data are nevertheless necessary, as will be apparent in the discussion.

The principal cases

The following cases are those which are used in support of the views expressed in the discussion.

Trachinotus falcatus (Linnaeus)

The presence of small black individuals in Sandy Hook Bay, New Jersey, was reported by Breder (1923) and noted by Nichols and Breder (1926). These were collected October 4, 1922, on a light sandy beach, littered with bits of weed and other debris. They were described as a smooth velvety black with hyaline fins. All were near 24 mm in standard length. Two were kept in an aquarium for a few weeks during

which time they became silvery,¹ resembling in color the much more abundant young of *Trachinotus carolinus* (Linnaeus). The latter vary very little from a generally silvery color, so far as known, except for becoming very dusky in certain aquariums, as is reported by Fields (1962) for sizes of from 15 to 30 mm. The two young *T. falcatus* differed from any of the small black fishes encountered in that the iris was a ruby red. Subsequent years others were seen at the same place, as noted by Breder (1926, 1928, and 1929). None of these exceeded 35 mm in s. l. and it seemed that they spontaneously lost the dark phase, usually at somewhat less than that size. The red irises always became silvery as the dark pigment waned.

Various regional lists, some published before the above notes but based on preserved material, include notes on other pigmentary variations in these small fishes: Meek and Hildebrand (1925) on Panama material; Hildebrand and Schroeder (1928) on material from Chesapeake Bay; and Fields (1962) on material from Massachusetts to Haiti. All show illustrations of this dark stage, the first of a 48 mm example still evidently quite dark, the second of an 18 mm fish and the third of an 16 mm fish. The following quotation is from the 1928 paper: "Very young (40 mm and less in length) densely punctulate with rusty dots, giving them the color of a dead leaf; dorsals and anal very dark; caudal pale." The 48 mm example is described as densely punctulate with dark points. There can be little doubt that at least some of these were very dark or black in life. Longly and Hildebrand (1941) mention rather similar coloration of a 15 mm individual taken in floating *Sargassum* at the Dry Tortugas, Florida, and that others from 9 mm to 11 mm varied in color from nearly black to brownish with dark punctulations and that the soft parts of the vertical fins were abruptly colorless. Randall and Randall (1960) reported individuals of about 16 mm, taken from St. John, Virgin Islands, in July, as black and bronze. These fish had the flexed tail and other typical behavior items Randall and Randall considered as causing them to resemble leaves. Fields (1960) described at length the many color variants these young fishes may display. Beebe and Tee-Van (1928), and nearly all authors with

¹Fields (1962) reported that similar silvery young placed in an indoor aquarium tended to darken, but would return to silvery if the aquarium was placed in direct sunlight outdoors. In a personal communication, Dr. Phyllis Cahn independently reported a similar reversible condition while working with this species at the Cape Haze Marine Laboratory.

comparative series, commented on the extreme variability of the young of this species.

Earlier these small sizes were reported as often common at Woods Hole, Massachusetts, from July to October (Sumner, Osborn and Cole, 1867). They make no mention of the coloration of the young, as their paper is limited to a list of forms found. Neither do other early lists of fishes from that area, such as Storer (1867), Baird (1873), Smith (1898), and Kendall (1908), nor the more general treatments of Goode (1884) and Jordan and Evermann (1896). However Bean (1888) gave a largely forgotten illustration of a dark colored *T. falcatus*, re-published by Fowler (1907). Both authors reported collecting small, dark colored examples at Beesley's Point, New Jersey, a favorite collecting site in those days. All of the fishes ranged from 1 inch to 2½ inches in length, presumably total lengths. Bean wrote, "An individual, 1½ inches in length, taken at Beesley's Point, September 2, was mainly silvery when seined, but on being placed in a small aquarium almost instantly became brown, the dorsal and anal nearly black. On the ventrals, the anal spines and the anterior tip of the anal fin, the usual vermillion shading into orange." All these cases mention few individuals compared with quantities of the constantly schooling *T. carolinus* that were usually noted as silvery, if color was mentioned at all. Fields (1962) discussed at length the color variations in the young stages of *T. falcatus* and compared them with the lack of such pronounced chromatic variety in both *T. carolinus* and *glaucus*. The *T. falcatus* mentioned by Breder (1962a), were collected on April 25, 1961, in Lemon Bay, on the Florida west coast. It was not noted in that publication that they were in a fully black phase. They were about 20 mm in s. l. This is the earliest date recorded for the appearance of the dark phase. By December on this coast the median length of *T. falcatus* is nearly 60 mm s. l. (Springer and Woodburn, 1960), and black ones are rare by October.

T. falcatus and *Chaetodipterus* often appear together. When both species are of the above-mentioned sizes and in the black phase there is sometimes some difficulty in distinguishing one from the other. Therefore, the following key is given. The non-metric characters in the key are sufficient to distinguish the two as they swim in an aquarium.

- A. Spinous dorsal highest in the middle, 4th spine longest, dorsal VII, 19-20; the spines appear as though radiating from a center; a long spine at angle of interopercle, clear and glass-like; pelvics

under and shorter than pectorals; caudal forked; a vertical from maxillary passes through eye, tangent to or before the pupil.

Trachinotus falcatus Text-fig. 1.

AA. Spinous dorsal highest at front, 1st spine longest, dorsal edge level in middle, 5th to 9th spines equal in length and parallel, dorsal IX, 23; no long clear spine on interopercle, except in the smallest sizes there are three short spines, the middle one at angle; pelvics in advance of and larger than pectorals, caudal bluntly pointed, eye behind a vertical from maxillary.

Chaetodipterus faber Text-fig. 2.²

Lagodon rhomboides (Linnaeus)

On October 30, 1959, along the shore of Lemon Bay, what appeared to be a piece of black "trash" resolved itself into a small fish of about 15 mm. The beach had been recently storm-swept of most litter. Only a few odd bits of black decaying leaves were noticeable. These approximated the size of the fish. The amount of disturbance incident to wading about in the setting of a small trap did not cause the fish to move off. It merely stayed fairly close to one leader of the trap. After some observations on its general behavior, it was dipped up in a small aquarium dip-net. The fish made no attempt to escape capture.

When placed in a large jar of water, it was immediately apparent, despite the nearly solid black pigmentation, that the fish was a young *Lagodon*. The caudal, posterior dorsal and anal tips and the pectorals were perfectly transparent. It held itself curved rigidly and maintained its position by activity of the transparent pectorals. Almost immediately it began to bleach and show the usual pattern of bars. On release it swam off slowly, but did not join an aggregation of similarly sized *Lagodon* that hovered about not more than four feet away. All these fish were in their light and sand-matching colors and therefore very difficult to distinguish. They were active, alert, and not to be caught by a small dip-net. When attempts at catching the fish were made they formed a temporary fright school.

Menticirrhus

The four Atlantic species of this genus, at least, appear to be very closely related and all

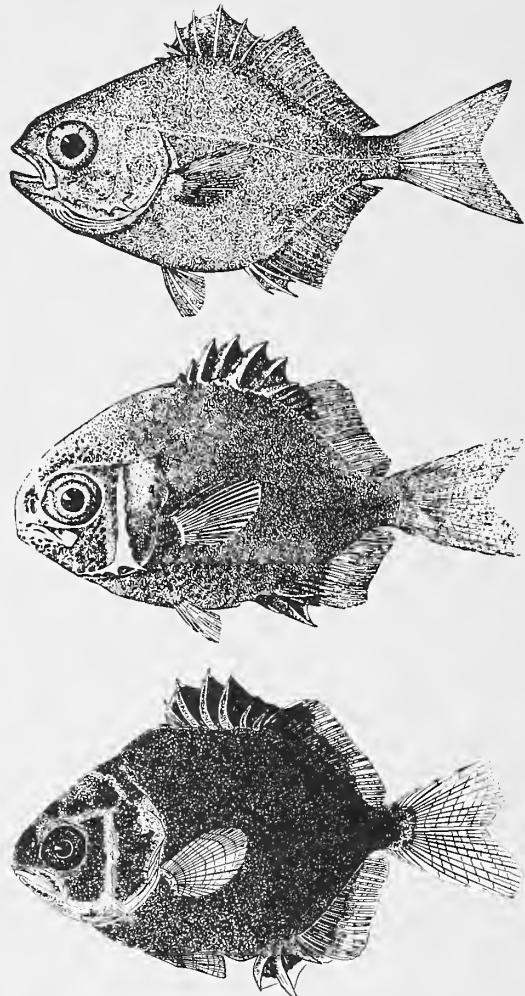
²The light nuchal band shown in this illustration is typical of this species when passing into or out of the black phase and is absent in *T. falcatus*.

of them have young which sometimes show melanism. Therefore the following sparse notes on the four species are treated together. All are commonly found in small aggregations in the 20 to 30 mm s.l. range, which usually do not number over two dozen individuals. They are distinctly fishes of light sandy beaches, typically in a light sand-matching color. The pattern of divergent bars, normal to some species, is frequently very faint or absent. Alternatively, they are found in a melanistic state, either as solitary individuals or usually as one black fish to a school. In no other species have black individuals been found in schools of otherwise lightly pigmented fishes. When alone they curve the body and do not attempt to flee, in the manner common to other species.

Menticirrhus focaliger Ginsburg. On November 22, 1959, shortly after the *Lagodon* was found, another nearly solid black fish of about 32 mm was seen not far from some fragments of "trash," near the same place. This fish resorted to immobility and made no attempt to elude capture. After being placed in an aquarium for closer scrutiny, there was no evidence of blanching, unlike the *Lagodon*. This fish displayed the posturing typical of the melanistic fishes. The caudal fin, pectorals and the posterior edge of the anal fin were fully transparent. The following morning the fish was as dark as when first found. It usually hovered near one of the corners of the aquarium, which were black on their interior surfaces. There was nothing in the aquarium but the fish and water. This fish seldom rested on the nearly black slate aquarium floor; it hovered in mid-water by use of its large pectoral fins, while the body and tail were mostly arched rather stiffly to one side. Fishes of the genus *Menticirrhus* normally sink to the bottom when not actively swimming, and unlike most other members of the family *Sciaenidae* they lack a swim bladder. It clearly took continuous physical exertion for the fish to keep itself away from the bottom.

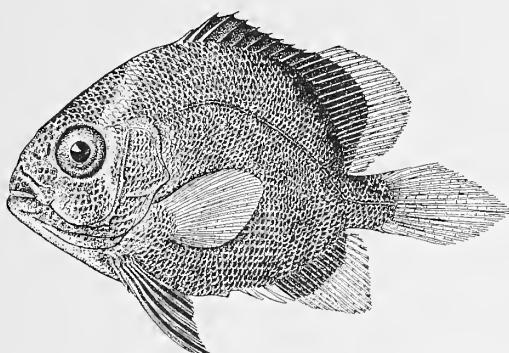
The lack of a tendency to flee from approaching objects was demonstrated nicely by this individual. When approached by a hand or a small stick, it merely stiffened the arch in its body and fluttered the nearly invisible pectoral fins faster. On very close approach of any small object, it backed away just far enough to escape physical contact.

The following day this fish was returned to the sea at the place it was found. It was still in the black phase and acted accordingly, staying at the place of release. The sea-floor litter was less abundant than at the time of capture. The fish was watched closely for about half an hour, during which time it appeared to be searching



TEXT-FIG. 1. *Trachinotus falcatus*. Three renderings of young fish in the black phase. Upper, after Bean (1888) circa 20 mm s.l. Middle, after Hildebrand and Schroeder (1928) 18 mm. Lower, after Fields (1962) 16.9 mm.

for a suitable place to station itself, moving about slowly, after the fashion of such fishes, and coming to rest some distance from various bits of trash, usually more than one foot distant. When it left the vicinity of one place, it would move along through open water, close to the bottom, head down and with the body turned partly on its side, almost precisely as has been described for much larger *Chaetodipterus* by Breder and Rasquin (1955). In about an hour the fish had vanished, which may mean that it had moved out of range or had simply disappeared within our visual range. The latter is not the least unlikely for in situations involving such backgrounds, obliteration of the fish is to be expected.



TEXT-FIG. 2. *Chaetodipterus faber*. Circa 20 mm s.l.
After Hildebrand and Cable (1938).

Springer and Woodburn (1960) mentioned the following, concerning fishes in the Tampa Bay area, "It was noticed that the young of *M. focaliger* under 22 mm exhibited two distinct types of color pattern. In one type the entire specimen except for portions of the fins is deeply and uniformly pigmented. In the other dark and light areas appear over the specimen in approximation of the adult coloration."

Dr. R. W. Harrington, who has collected many small shore fishes on the Florida east coast, wrote as follows in a personal communication in connection with these pigmentary conditions. "Have never seen coal-black *Lagodon rhomboides* but I have collected one small *Menticirrhus saxatilis* that was dark brown among a large group of *M. littoralis* which were pale, over a sandy bottom."

Many authors not concerned with the present interests have had occasion to note the dark phase of these fishes. Hildebrand and Cable (1934), for instance, not only mention, but also figure dark individuals of similar sizes of *M. americanus* (Linnaeus), *M. saxatilis*, and *M. littoralis* (Holbrook).

Menticirrhus saxatilis (Linnaeus). Earlier notes on this species, not concerned with pigmentation, yielded the information given in Table I and in Text-fig. 3. These notes, on fishes in Sandy Hook Bay, New Jersey, were used in part by Nichols and Breder (1926) for other purposes. As suggested in Table I, there were successive waves of young fishes entering the bay from later spawnings, which accounts for variations in the graph shown as Text-fig. 3. Especially marked is the small isolated group in October which has not been integrated into the other data because of its obvious difference in range of sizes. Although no records were kept at this time on the numbers of black individuals encountered, it was noted that they were

found only in the smaller sizes, between 10 and 30 mm, and were few in number. This agrees well with the descriptions and figures of Hildebrand and Cable (1934), who in presenting life history data showed that the dark phase was found in stages down to 10 mm but that this phase disappeared when the fish reached from 30 to 35 mm in length. Hildebrand and Cable made the following comment: "All the specimens at hand were caught among black, partly suspended vegetable debris, which they resemble in color. It seems probable that these fish are darker than they would have been had they been taken in a different environment." In another place they wrote, "The spinous dorsal and ventral fins are black; the pectoral fins are colorless; the second dorsal and anal have at least a partly black base, the rest of these fins being colorless; and the caudal is colorless, except for a black blotch on the base . . ." This statement could stand almost unaltered for any of the various species of small black fishes discussed here. Similar comments were made for both *M. americanus* and *M. littoralis*. Evidently these two species may pass through the black phase at just about the same sizes as does *M. saxatilis*. This seems to also apply to *M. focaliger*. Apparently the black stage appears only in the presence of blackish fragments of trash in the sea. Dr. D. E. Rosen, in a personal communication, stated that on the south shore of Long Island, New York, he saw a black *M. saxatilis* become light sand color in a moment.

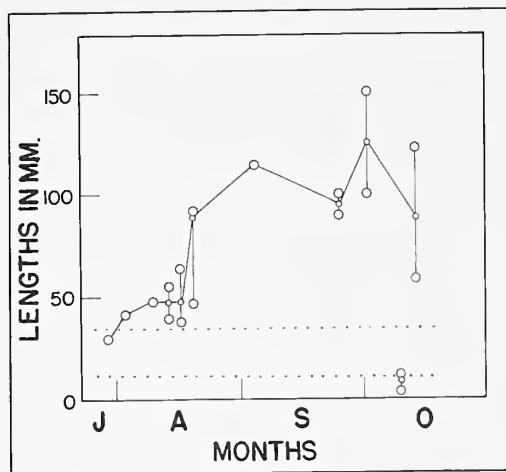
Chaetodipterus faber (Broussonet)

This species is the only one that has been studied in any detail in respect to melanism as a normal reactive process. Also it happens to

Table I.

OCCURRENCE BY DATE AND SIZE OF YOUNG
Menticirrhus saxatilis IN SANDY HOOK BAY,
NEW JERSEY

Date	Number of spec.	Standard lengths mm		
		Min.	Mean	Max.
1923				
Aug. 2	1	—	42	—
9	1	—	48	—
16	3	38	48	64
19	17	47	89	92
1924				
Oct. 9	4	4	9	12
19	80	58	89	123
1925				
Sept. 24	25	90	95	100
1926				
July 29	2	29	29	30
Aug. 13	2	39	48	55
Sept. 3	1	—	115	—
Oct. 1	15	100	125	150



TEXT-FIG. 3. *Menticirrhus saxatilis*. Presumptive growth curve based on data from Sandy Hook Bay, New Jersey, in Table I, 1923 through 1925. Large circles indicate extremes of size range or single fish in s.l. Small circles indicate means of sample. See text for explanation of group near base line in October. The range between the two dotted horizontal lines shows the sizes at which the black individuals may be expected.

have a fair amount of its life history recorded. Therefore the treatment here has been extended in order to establish more fully the relationship of inverse pigmentation to development and life history.

Spawning clearly takes place in spring and is earlier southward. Reproductive activity is not known north of Virginia, but individual fishes are found as stragglers, especially in the late summer, to Massachusetts, but not north of Cape Cod. The eggs are buoyant, non-adhesive, and average about 1.25 mm in diameter. They hatch in about 24 hours at a temperature of 80° F, according to Ryder (1887). All indications are that spawning takes place well offshore. As noted above, Hildebrand and Cable (1938) found small fry offshore but none were found under about 15 mm in inshore waters near Beaufort, North Carolina. Twenty-eight hours after hatching the larvae measure about 3.5 mm and evidently show no indication of any pigmented over-development. Nor does anything indicate that Ryder had any knowledge of the black phase, which first appears at about a length of 9 mm as indicated by Hildebrand and Cable.³ Strangely, Ryder noted that the larvae

might be phosphorescent, a condition which no one since that time has mentioned, but apparently no one has had living larval *Chaetodipterus* since then.

Springer and Woodburn (1960) indicated a spring and summer spawning season in the Gulf of Mexico, a condition which all our data supports. The data of Gunter (1945), Reid (1945), and Springer and Bullis (1956), together with their own material and collections, lead Springer and Woodburn to believe that *Chaetodipterus* in the Gulf spends its winter season mostly in offshore waters. We differ in no way with this view, based both on present work and prior experience in Pine Island Sound in the 1930s. Kilby (1950) and Reid (1954) both took small individuals running from 20 mm to 30.5 mm in length, at Cedar Key in June and July and one in December of 46 mm. Springer and McErlean (1962) took examples at Matacumbe Key during October, November, and December that averaged 25 mm, 36 mm, and 42 mm respectively.

The black phase of *Chaetodipterus* was first described in detail by Breder (1946). The fishes reported then were nearly all of a size of about 9 mm. They were collected on the following dates in 1942 in the quantities indicated below.

June	11	2
	12	4
	13	5
July	3	1
	5	1

A few others were seen on the above days. No others had been seen on four previous summers in the same place, Palmetto Key, Pine Island Sound, Florida. In view of their subsequent rather erratic appearance at other places, it may be that the real reason for not seeing them before 1942 at Palmetto Key was this erraticness, and not, as thought at the time, merely because of their inconspicuousness against the background on which they were found. After June 11, noted above, these little fishes were sought energetically every day to July 11, with no success after July 5.

Similarly there is great variation in the numbers of small black *Chaetodipterus* which appear at Siesta Key from one season to another. The numbers which appeared there in 1962 far exceed those of any other year or at any other known location where they may be found. This comment is based on the combined observations of a number of persons, chiefly Dr. E. Clark, from 1960 through 1967. Fortunately in the year of greatest abundance it was possible to have the assistance of Mr. Louis Godey, whose notes have yielded the general frequency in

³None of the earlier papers mentioned under *Trachinotus* noted anything about the black phase of *Chaetodipterus*.

time, which is given in Table II, as well as their general distribution, which is shown in Text-fig. 4.⁴ According to Dr. Clark, the two previous years were notable for the general presence of considerable numbers of fishes in the black phase. After that time, although fair numbers were present in 1963, the total fell off to a single fish caught in 1967. That year Mr. Fred Small, of the Mote Marine Laboratory staff, reported some of these fishes on Anna-Maria Key, but that was all. Collecting efforts were continued through 1967, but radically fewer fishes were seen.

The large influx of small black *Chaetodipterus* along the Gulf shore of Siesta Key is evidently influenced by the local configuration of the shoreline, but is probably primarily established by the nature of the circulation of Gulf water. Chew (1955) defined a convergence mechanism on the Florida west coast which, with the off-shore circulation, apparently produces a shore concentration of water-borne materials. He holds this effect responsible for the shoreward movement of the "red tide" and the fish kills that result. At the time of these concentrations of black *Chaetodipterus*, there was no "red tide." Such small fishes are among the first destroyed in the area of an outbreak of this toxic phenomenon.

Table III shows that the black phase was not seen on the Gulf coast of Florida earlier than April 26, nor later than October 18, while on the Atlantic side the black phased individuals were first observed on June 6 and the latest on August 16. These data do not suggest any marked seasonal differences in the time of appearance of the black phase between the Gulf and Atlantic sides of Florida. The smallest fish in the black phase seen on the Gulf side was 8.2 mm in length; on the Atlantic side it was approximately 9 mm. The largest in the black phase in the Gulf was 74 mm, and none nearly that size have been reported from the Atlantic coast. Much of this is evidently a matter of insufficient records. In the Bahamas, the black phase occurs in fish at least up to 300 mm in length, while the smallest reported in black phase is 76 mm long.

The following additional instances are given to clearly indicate that this type of behavioral and physiological melanism, while erratic in local appearance, is not a particularly rare phenomenon.

Reid (1954) reported that young of approxi-

mately 20 mm were taken at Fort Myers Beach and, "... were colored a rich black, and with a perfectly transparent caudal fin, were found very close to barnacle-covered piles. These were also as close to floating wrack . . .".

In a personal communication, Dr. R. W. Harrington reported as follows: "Saw *Chaetodipterus faber* June 6, 1955, in shallow water over a mixed sandy and flocculent bottom to one side of the mouth of the canal (large ditch) draining our laboratory, Entomological Research Center, Vero Beach, Florida, i.e., where the canal debouches into the shallows of the Indian River. I recall how hard they were to see and how dark they were, but have no further notes. We were able to take only three in the seine (range 16-32 mm s. l.) and have collected only one specimen since (in a shallow turbid embayment of Indian River transected by the St. Lucie County line, among patches of algae, *Halodule*, and *Ruppia*, June 7, 1956, 18 mm s. l.)"

The following cases of the occurrence of similar small black individuals were reported by Dr. Clark.

Gasparilla Island. Seen on the Gulf side in about eight feet of water, September 1955. Aside from the North Carolina records (Hildebrand and Cable, 1938) of specimens collected near the bottom by tow nets, which surely occurred in much deeper water, the above seems to be the deepest that these black-phased specimens have been collected. These authors noted that all young fish under 15 mm were taken in outside waters.

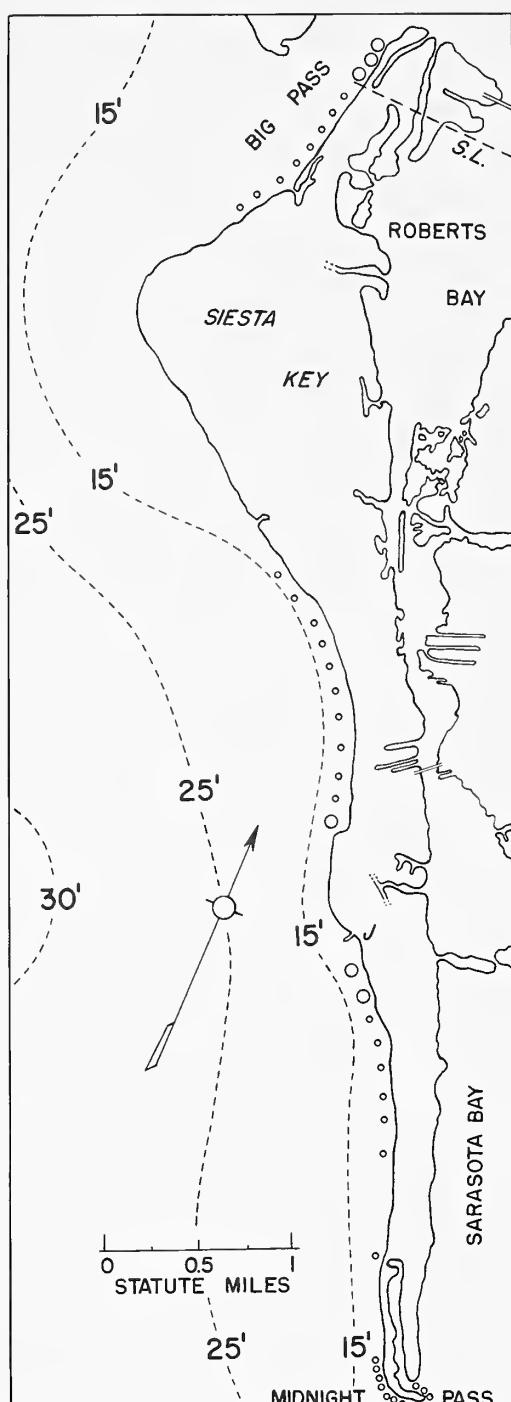
Table II.
OCCURRENCE OF YOUNG *Chaetodipterus* IN THE
BLACK PHASE ON SIESTA KEY, FLORIDA,
DURING 1962

Date	Nos. seen ¹
July 1	0
2	0
5	2
12	10/sq. ft.
Greater numbers were seen between the above date and the following:	
Aug. 1	10/sq. ft.
6	1
8	2
12	0 ²
14	0
15	1

¹These observations were all made at the localities indicated in Text-fig. 4.

²During Aug. 11 and 12, "large numbers" were reported from Sanibel Island.

⁴With the *Chaetodipterus* were some similar sized *Trachinotus falcatus* also in their black phase, but they were not numerous. See also under that species for related data.



TEXT-FIG. 4. Distribution of small black phased *Chaetodipterus* at favored locations on the Gulf coast of Siesta Key, Florida, during the 1962 summer, one of unusually great abundance. S. L. indicates the southernmost city line of Sarasota. J. indicates jetty where much of the work was done. Water depth is as of mean low tide, in feet. Large circles along shore indicate concentrations of over 10 fish per square foot of bottom. Small circles indicate scattered individuals. See text for details.

Mote Marine Laboratory (Siesta Key). At this locality black-phased *Chaetodipterus* were seen each year as indicated earlier and usually some *Trachinotus falcatus*.

Table III lists the sizes found with related dates, locality, and the sources of information. These are from the literature and by way of personal communication, while entries without source indication are new. Total lengths are used throughout unless otherwise noted, but many of the older references do not specify their usage. For present purposes these differences are not critical. Appropriate information in Table III, plotted against time, forms a generalized presumptive growth curve and is shown as Text-fig. 5. Although the data ranges from Texas to New Jersey, a not unreasonable growth curve is suggested.⁵ Other data, including that of the occurrence of gravid females and breeding males, are also indicated. With this condensed life history data as a background, the range of occurrence of the black phase is indicated. None over a length of 35 mm have been found in the comparatively turbid water of Florida's Gulf coast, but in the clearer waters of the Bahamas the black phase and the accompanying characteristic attitudes have been found in fishes up to 300 mm. The lack of the young of the year in the Gulf shore area during fall may support the view of Springer and Woodburn (1960), and others, concerning an offshore movement of the species in cooler weather.

The black-phased individuals have always been seen as solitary fishes, except for the following cases. The first was discovered by Dr. Clark and her daughter on Siesta Key during 1959 when the fish were most abundant. Then young black-phased *Chaetodipterus* were sometimes seen in "clusters" of a few to about 20 individuals. These tended to be grouped either in contact with each other or very close together, with tails toward each other. Each fish

⁵ It is to be noted that *Chaetodipterus* does not grow to as large a size in the Gulf of Mexico as it does on the Atlantic coast. Gunter (1945 and 1950) indicates and discusses this condition, having found no fishes over 195 mm after years of observation, while Hildebrand and Schroeder (1928) reported fish up to 12 lbs. in Chesapeake Bay. Nothing is known of the relative growth rates.

faced outward in a different direction. They looked very much like a spray of dead and blackened weed and could easily escape notice.⁶ The fishes seemed to be just about at the size where hostility is replaced by schooling, and at the end of the black phase. These groups may be in a short-lived transitional state, which could account for them being so seldom seen.

Another, but different case of non-solitary black *Chaetodipterus* was reported (Townsend, 1929) to have occurred in the New York Aquarium, when it was located at the Battery. A fully adult *Chaetodipterus* became uniformly black after being placed in an aquarium containing similarly sized *Pomacanthus aureus* (Bloch). When returned to the company of its own kind, it promptly took on the more usual banded phase. There has been no opportunity to check this further with other individuals, but it is in accord with present data and those of Breder and Rasquin (1955).

Reid (1954) reported that, "When disturbed the fish darted among the barnacles; if the escape route was blocked they would remain motionless and could be caught easily by hand." Evidently these fishes were in open water, above or beside the barnacle beds, which may account for the difference in behavior from those close to an open sandy beach.

Other cases

The following accounts cover species in which the black phase is only slightly known.

Mycteroperca and *Epinephelus*

These two genera of groupers, known for extensive pattern changes, contain species which include in their repertoire of phases, one which is almost if not quite as black as those of the fishes previously discussed. Such black phases are mentioned and figured by Townsend (1929) for *E. morio* (Valenciennes) and *striatus* (Bloch) and for *M. bonaci* (Poey). The significance, if any, to the present studies is not clear. These fishes habitually change their patterns and colors, apparently more in reference to social behavior than to background.

Lobotes surinamensis Bloch

The adults of this species are commonly very dark and often quite black. The New York Aquarium often obtained specimens from the

lower New York Harbor, one of which is shown in Gudger (1931). The young display beautiful leaf mimicry and often aggregate with yellowed mangrove leaves (Breder, 1946 and 1949b).

Platax orbicularis (Forskal)

This species is often described as closely resembling yellowing leaves, in both form and color, e.g. Willey (1904), Mortensen (1917), and Randall and Randall (1960). The last described behavior rather resembles that of *Chaetodipterus*, but the color was not black. When seen in aquaria, in the United States, they are very apt to be solid black.

Abudefduf taurus (Muller and Troschel)

A single individual was seen in the black phase by Dr. T. N. Tavolga near the Marineland Oceanarium, St. Augustine, Florida, in July 1952. His personal communication read, "It was placed in an aquarium, where it took two days for it to fade sufficiently for the normal pattern to become visible. The fish was about 15 mm s. l."

Tautoga onitis (Linnaeus) and *Tautogolabrus adspersus* (Walbaum)

The young of these species are frequently found in a very black state from about New York Harbor northward. So far as known these all seem to be found in close association with notably black bottom materials, just as when found as bright green fishes associated with bright green plants, such as *Ulva*.

Monacanthus sp.

An individual of less than about 25 mm in length, in a coal black state, was seen near the surface amid some sea wrack, in Lemon Bay, Florida, in July 1967. It eluded capture by simply "disappearing." Mortensen (1917) includes this genus in those black forms he found floating in the sea amid blackened bits of wood.

Stathmonotus hemphilli Bean

This species is capable of considerable pattern change, although living cryptically for the most part. When in a nearly completely black phase, it will rest in the open on a light background, at least in an aquarium (Breder, 1949a).

Histrio, *Antennarius*, and *Ogcocephalus*

These genera are all capable of taking on a black phase (see Breder, 1949a and Breder and Campbell, 1958). The first two are definitely background-matchers and have not been found on a non-matching background, but the third is often seen in a completely black phase on light sandy bottoms.

⁶ Dr. Clark also reported occasionally finding groups of these fishes that were remarkably similar to a spray of living sargassum weed in both general outline and coloration. This algae is not a very common floating element at this place, but there was some about at the time these fish groups were seen.

Table III.

PERTINENT DATA ON *Chaetodipterus*

For each entry the collector or authority is given on the left side, following day and year. The numbers and total lengths in mm of specimens are given when known, unless otherwise indicated, under the reference name. The location and condition of the specimens is given at the right hand side. The tabulations are chronological by months. P. C. indicates "Personal communication."

APRIL			
26/24	E. Clark (P. C.)		Siesta Key, Florida
	1	Small	Black
MAY			
26/16	Hildebrand and Cable (1938)		Beaufort, N. C.
	—	—	Females with advanced eggs
26/16	Hildebrand and Schroeder (1928)		Crisfield, Md.
	—	—	Females with advanced eggs
31/44	E. Clark (P. C.)		Ft. Myers Beach, Fla.
	1	24 s.l.	Black
5/64	E. Clark (P. C.)		Siesta Key, Fla.
	6	—	Black
13/64	E. Clark (P. C.)		Siesta Key, Fla.
	Many	Small	Black
JUNE			
Early	Smith (1907)		Beaufort, N. C.
	—	—	Ripe males and females
4/64	E. Clark (P. C.)		Siesta Key, Fla.
	—	Small	Black
6/55	R. W. Harrington (P. C.)		Indian River, Vero Beach, Fla.
	3	20-30	Black
6/58	Springer and Woodburn (1960)		Tampa Bay, Fla.
	2	8.2-8.5	
11-13/42	Breder (1946)		Pine Island Sound, Fla.
	11	9±	Black
14/60	Gunter and Ward (1961)		Wine Island, La.
	1	38±	—
19-20/63	E. Clark (P. C.)		Sarasota Pass, Fla.
	3	Small	Black
21/24	Breder (1946)		Pine Island Sound, Fla.
	1	—	Ripe male
25/63	Kitty Paul		Siesta Key, Fla.
	5	11-25	Black
-/48	Reid (1954)		Cedar Key, Fla.
	1	20	Black
JULY			
1/61	E. Clark		Siesta Key, Fla.
	50±	5.5-25 s.l.	Black
3-5/42	Breder (1946)		Pine Island Sound
	2	9±	Black
4/61	E. Clark		Siesta Key, Fla.
	69	6-24 s.l.	Black. Great numbers seen
7/56	R. W. Harrington (P. C.)		Indian River, Vero Beach Fla.
	1	23	Black
9/58	Springer and Woodburn (1960)		Tampa Bay, Fla.
	3	19-25	—
9/29	Fowler (1931)		Port Aransas, Texas
	1	37	Banded
9/30	Hildebrand and Cable (1938)		Beaufort, N. C.
	1	9	Apparently black
9/64	S. Page		Manasota Key, Fla.
	2	Small	Black

11/29	Hildebrand and Cable (1928) 1	2.5	Beaufort, N. C. Larval
12/15	Hildebrand and Cable (1938) 1	4.25	Beaufort, N. C. Apparently black
12/14	E. Clark (P. C.) 1	25 s.l.	Ft. Myers Beach, Fla. Black
20/46	Breder (1948) Several	Mature	Bimini, Bahamas Black, countless banded
21/62	L. Godey (Records) 8	18-32 s.l.	Siesta Key, Fla. Black
-/49	Reid (1954) —	—	Ft. Myers Beach, Fla. Black
-/48	Reid (1954) 1	33.5	Cedar Key, Fla. Black
Mostly 6 & 7/41-42	Gunter (1945) 44	62-195	Bays & Gulf, Texas —
AUGUST			
4/58	Springer and Woodburn (1960) 1	10	Tampa Bay, Fla. —
16/16	Hildebrand and Cable (1938) 1	17	Beaufort, N. C. Apparently black
23/30	Hildebrand and Cable (1938) 10	49-62	Beaufort, N. C. Some barred, others probably black
25/43	E. Clark (P. C.) 2	15-20 s.l.	Ft. Myers Beach, Fla. Black
25/56	E. Clark (P. C.) 1	15 s.l.	Manasota Key, Fla. Black
29/57	E. Clark (P. C.) 4	18-30 s.l.	Siesta Key, Fla. Black
Late	Smith (1907) —	73±	Beaufort, N. C. —
SEPTEMBER			
3/58	Springer and Woodburn (1960) 1	10.1	Tampa Bay, Fla. —
4-6/30	Hildebrand and Cable (1938) 21	57-86	Beaufort, N. C. Some with bars, dark or light
18/55	Hildebrand and Schroeder (1928) 1	55	Chesapeake Bay, Md. —
OCTOBER			
2/22	Hildebrand and Schroeder (1928) 8	69-83	Chesapeake Bay, Md. —
3/58	Springer and Woodburn (1960) 1	16.8	Tampa Bay, Fla. —
3/24	Breder (1925) 1	300±	Sandy Hook Bay, N. J. Banded
7/22	Hildebrand and Schroeder (1928) 1	78	Chesapeake Bay, Md. —
8/30	Breder (1931) 1	457	Sandy Hook Bay, N. J. —
11-13/22	Hildebrand and Schroeder (1928) 2	80-100	Chesapeake Bay, Md.
18/21/30	Hildebrand and Cable (1938) —	72-74	Beaufort, N. C. Some banded, dark or light
18/61	Kay von Schmidt (P. C.) 1	32 s.l.	Siesta Key, Fla. Black
23-23/15	Hildebrand and Schroeder (1928) 12	65-85	Off mouth of Potomac River —
-/48	Kilby (1955) 1	20	Cedar Key, Fla. —
-/60	Springer and McErlean 4	19-31	Matacumbe Key, Fla. —

NOVEMBER			
8/57	Field notes (original)		Pine Island Sound, Fla.
	Many	250±	Bands strong
-/-/60 Springer and McErlean (1962)			
	11	32-45	Matacumbe Key, Fla.
-/-/60			
DECEMBER			
3/43	Breder and Rasquin (1955)		Bimini, Bahamas
	1	76±	Black
-/-/48 Reid (1954)			
	1	47	Cedar Key, Fla.
-/-/60 Springer and McErlean (1962)			
	2	37-45	Black
			Matacumbe Key, Fla.
			-

Gymnochirus melas Nichols

The young of this species, up to about 50 mm, will rest on a light bottom under illumination and show a fully black phase. In darkness this species changes to a slightly lighter cross-barred pattern, but is still a very dark fish (Breder, 1955). The figure of a dark-conditioned fish of about 20 mm s.l., with its bars showing, given by Breder (1955), agrees well with that of a preserved fish of about 31 mm given by Dawson (1964), who clarifies the relationships of this genus.

Lepisosteus osseus (Linnaeus)

A note from Dr. C. L. Hubbs, in Breder (1964), indicates that sometimes young individuals of one to three cm, are found associated with decaying twigs and leaflets. These were a sooty black, which closely matched the litter.

The above is the only case which possibly may belong to this group, which is not included in the Teleostei. It is, of course, a member of the Holostei, generally accepted as ancestral to the more modern Osteichthyes.

EXPERIMENTAL PROCEDURES

Experiments were carried out in order to establish certain points not obtainable by simple field observations and to check earlier work. See Breder and Rasquin (1955) for experiments not repeated here.

Plastic basins

Conventional glass-sided aquaria are not satisfactory containers for the study of pigmentary changes under consideration here, because of the vertical black angles in each corner of the aquaria. Rectangular white polyethylene basins with rounded corners, measuring 14½ x 12½ x 5½ inches deep, were found to be completely satisfactory for these purposes. Since such containers are slightly translucent they were kept on a clean white surface to avoid any possible

darkening of the lower portion. All fishes used were transferred to the basins directly from the traps in which they were caught. With these traps it was possible to do this without removing the fishes from the water at any time. They have been described by Breder (1960 and 1962a). These experiments were carried out in 1960.

Fishes Known to Have a Contrasting Black Phase.

Trachinotus falcatus

Two individuals studied April 25 to 26. Each fish was placed in a separate basin. One basin held two pieces of black paper, a circular piece $\frac{5}{16}$ of an inch in diameter, and a larger, roughly rectangular piece. In the other basin were two circular pieces of paper identical to the circular piece in the first basin. The two fishes behaved in the typical fish manner, remaining substantially inert and seemingly indifferent to the approach of hand or net. A demonstration of their quiescent manner is given in Plate 1, Figs. 1, 2, and 3. The first figure shows the normal undisturbed fish, stationed some distance from the black marks. Here the distances are less than are usual in the sea; this fact may have some relationship to the size of the available swimming space or to the distance between the only black objects present. In the second figure a small net has been thrust under the fish. It can be noted that the fish is in a slightly different position than in the first picture. This was caused when the net accidentally touched the fish. Immediately, on the removal of the net, seen in the second figure, a hand was thrust into the water, as is shown in the third figure. The fingers wiggled continually, which the surface ripples indicate. The fish, between two of the fingers, retained its position throughout the disturbance. The behavior of the black fishes in the sea is indistinguishable from that here described in the basins. Similar sized fishes in a light and more or less background matching

phase dash about violently under identical treatment.

Lagodon rhomboides

Six light colored individuals were studied from March 16 to April 7. These showed at no time any suggestion of responding to any dark spots. The six fishes used were studied two at a time, each in a separate basin, so that each fish was always alone. Most of the time the fish rested in a more or less curved position, either in a very light phase or with a faint barred pattern. They always showed violent agitation on the slightest approach. It seems that here the chromatic reactions are not especially linked to the background, but rather to their internal states in respect to fright or stress. There was some attempt at background matching but it obviously was not complete. The curved pose may be somewhat related to temperature for it was more in evidence when the water temperature fell to below 72° F. During this series of observations the temperature of the water ranged from 58° F to 82° F. Also in cold water the fishes stayed in the shadow of the rim of the basin whenever possible. This reaction is in accord with Barlow (1958) and Breder (1959), both of whom indicated that various fishes will become light-negative when water temperature lowers through some threshold value. The black example of *Lagodon* discussed in the preceding section, is the reason for including this species here.

Fishes Not Known to Have a Contrasting Black Phase.

Eucinostomus gula (Quoy and Gaimard)

Nine fishes of about 15 mm were studied from Nov. 3 through 19. These were introduced into a basin as small fry, too young to be identified certainly in life. Recognizable characters developed before this series was terminated and they were held further in an aquarium for confirmation. This was possible because a characteristic black tip develops on the dorsal, involving the membranes of the longest dorsal spines, entirely unlike any other small fish in this body of water. This becomes easily noticed by the time they are about 20 mm s. l. During their sojourn in the basins they lived in a fairly close group and generally cruised about or rested quietly in a corner. At no time did they show any evidence of reacting to the dark spots. Throughout this period they maintained the lightest phase seen in this species and size, a little lighter than in fish taken over a clean sand beach. The development of the black dorsal tip is evidently independent of the background reactions of this species.

Sciaenops ocellata (Linnaeus)

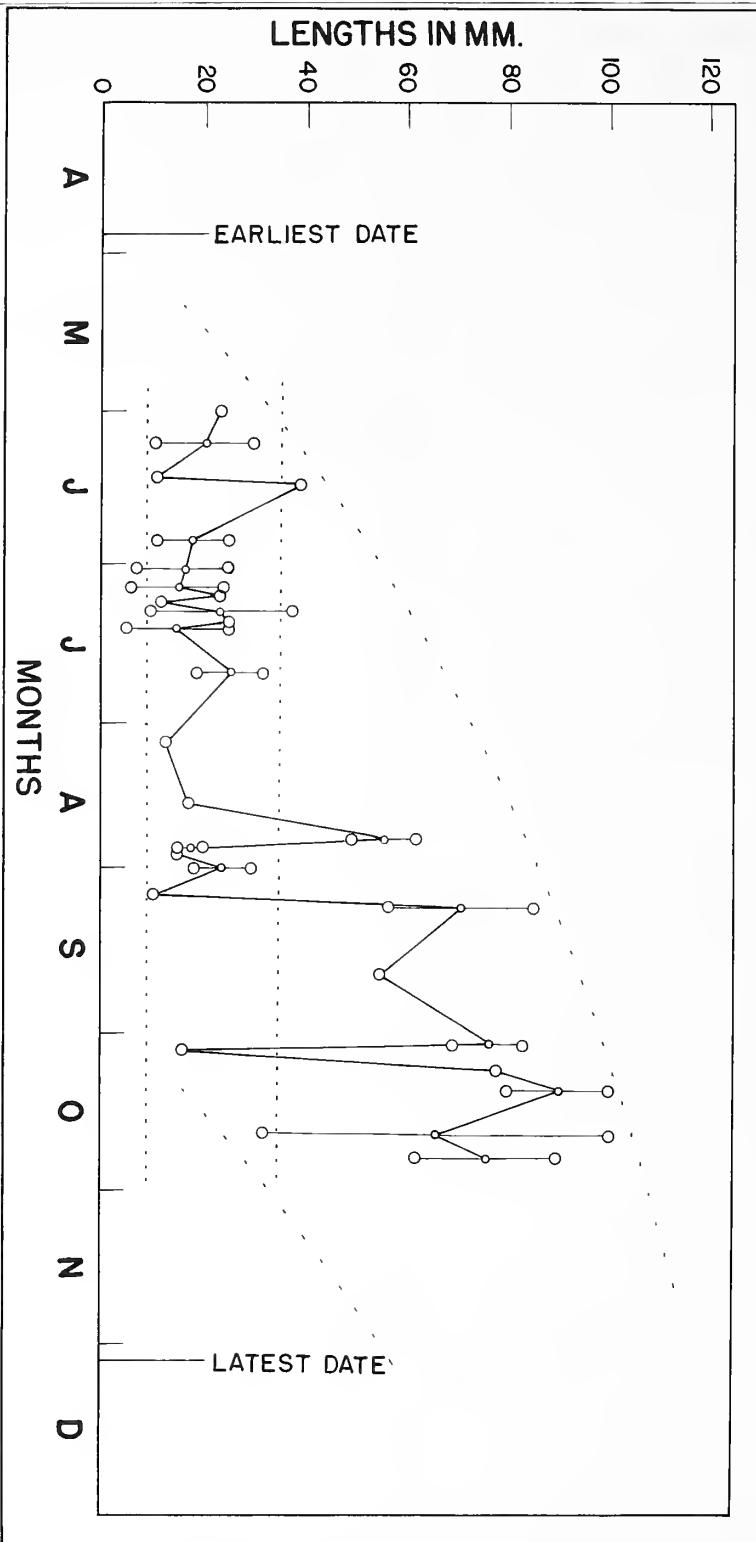
Six fishes of about 28 mm s. l. were observed from Nov. 10 to 18. When exposed to the environment of the basins, this species responded in a way unlike any of the others to the black spots. Although they took on a very pale phase when placed in the light basin, typically they would rest their heads on a black spot. This act of placing the head on a black spot was immediately registered by the darkening of the melanophores, roughly in proportion to the amount of retina covered by the spot's optical image—that is, it was related to the precise positioning of the head. If the head was not placed on the spot the darkening would be in approximate ratio to the nearness of the spot, if it were not more than about one-half inch distant. Fright would cause the fishes to leave the spots in haste, usually to "hide" on the side nearest the disturbance, where it was impossible for them to see the intruder. Both circular and rectangular spots were so utilized. Early in the morning these fishes were always lighter and usually not on their spots, but as day brightened they returned to them. Evidently they prowled about during the night, apparently in search of food. It would appear that intense light influences this species, at this size, to seek darker backgrounds.

Syphurus plagiusa (Linnaeus)

A single fish of about 22 mm s. l. was observed from Nov. 11 through 18. This individual behaved as could be anticipated for practically any flatfish, responding promptly to background and matching it as well as possible within the limits of its chromatic equipment. That is, in a white basin with no black spots it would all but disappear, except for its black pupils. Being still a very small fish at these times, it had the advantage of being virtually transparent. When a dark spot was present and in the fish's visual field, the fish, darkened roughly in proportion to its distance from the spot, showing reactions similar to those described for *Sciaenops*.

Variable light aquarium

In order to have flexibility in the use of light for these studies, a special illuminating arrangement was provided. An aquarium constructed of clear sheet plexiglas, one-quarter inch thick, held together only by transparent cement, was employed. It lacked the dark corners of conventional aquaria, a needed feature for reasons already explained in connection with the plastic basins. The aquarium measured 18 x 12 x 12 inches, outside dimensions. It was placed on a table with a glass top measuring 24 x 15½



TEXT-FIG. 5. *Chaetodipterus*. Presumptive growth curve based on data from various sources. The range between the two dotted horizontal lines shows the sizes at which the black individuals may be expected on the Atlantic and Gulf coasts. In the Bahamas the black phase may be found at much larger sizes. See Table III and text for full explanation.

inches. A light frame, supported by a single rod from each corner of the table, was constructed to hold whatever overhead illuminating fixtures or other equipment might be needed. Below the table a light-tight plywood enclosure, of inverted pyramidal shape, was placed, with its base the glass table top and with a light socket at its apex, the low point, being near the floor. The plywood was lined with aluminum foil as a reflector and ventilated so that a small motor driven blower would prevent the aquarium from over-heating.

Running sea water entered and left the aquarium by glass tubes, thus providing no dark spots within the view of the fishes.

Translucent white paper was placed under the aquarium, on the glass table top, so that the under-lights presented a uniform illumination from below. A similar paper was placed under the overhead lights. The aquarium could be surrounded by any color of paper or cardboard called for. A further protection could be had by stretching sheets of paper or a cloth curtain between the four uprights supporting the overhead lights.

It was thus possible to give the fish confined in the aquarium uniform illumination, either from above, below, or both, in any combination of intensity from none to the full amount the bulbs could deliver (a matter of 150 footcandles in the center of the aquarium from both directions). Thus the overhead light alone, with its reflection from the bottom and sides would give a normal albedo, dependent only on the reflectivity of the surfaces and the clarity of the water. The added use of the underneath lights could provide "albedoes" greater than the bottom, of whatever nature, could reflect. It could be brought to, for instance, an impossible "albedo" of 1.0, or even beyond, by suitable manipulations.

Much work has been done attempting to demonstrate that fishes in adjusting their pigmentary systems are in fact responding to the albedo. See Walls (1942), Parker (1948), Odiorne (1957) and Fingerman (1963) for reviews. This is the ratio of reflected light, R , to that of the incident light, I , from the bottom. Thus albedo = R/I , which is usually expressed as a decimal. The validity of this work on albedos is not universally accepted and, as it developed, it does not bear directly on present considerations. Through the use of this equipment however, it became possible to delimit some of the parameters controlling the occurrence of the black-fish phenomenon, which follow.

1. Water sufficiently clear and shallow to permit good light penetration.

2. Illumination sufficient to make item 1 possible.

3. Location at or near primarily light bottoms or at the water surface,⁷ but not at intermediate depths.

4. The presence of inert dark colored, typically black objects of appropriate size, resting on the bottom or floating.

Item 2, above, implies that in times of darkness the melanism should slowly lighten. The speed of this process is proportional to the original density of the melanophores. Item 3 is based on the fact that all observations have been made in these places. The reason for this is implied in item 4, as most submerged inert objects all either sink or float. Few are close enough to the density of water to have neutral buoyancy. As used here, the word "inert" does not imply lack of motion, for often slight wave action will move the lighter materials which rest on the bottom in a somewhat rhythmic manner. The floating materials are usually in motion with the surface waters.

Tests of the operation of the variable-light aquarium were made with *Oligoplites saurus* (Bloch and Schneider), *Gambusia affinis* (Baird and Girard), and *Poecilia (Mollienesia) latipinna* (LeSueur). These fishes all behaved exactly as expected. The two poeciliids reacted in accordance with the studies of Sumner (1935) on *Gambusia*. *Oligoplites*, the young of which resemble leaves (Breder, 1942), the only carangid so far studied in a variable-light aquarium, was not surprising in its reactions, but as the details of the reactions have no bearing on the present studies, they are not reported here. In no case did any of these fishes show any distress following full illumination from below for as long as a day. A sudden change in the illumination intensity would sometimes result in one or more of the fishes giving a slight momentary "start," but nothing more.

Chaetodipterus faber

A single individual of 50 mm s. l. was placed in the aquarium described above on August 31, 1967. This fish was in a thoroughly black state.

⁷ Mortensen (1917) considers the case of various small fishes swimming amid floating fragments of blackened wood, which is clearly the closest mention in the earlier literature to the black fish problem, as understood here. *Lepisosteus osseus*, mentioned earlier, is evidently a fresh-water version of the same thing. Cott (1940) in his large treatise, essentially a catalogue of instances of alleged protective coloration, gives no reference to anything equivalent to such cases. The present examples behave in a manner similar to his "Aposematic" animals, exposing themselves freely and showing sluggish movements.

It had been caught during some seining operations of the Mote Marine Laboratory and before being introduced into the experimental aquarium lived at the laboratory in a large tank with several kinds of larger fishes for about a week. It was not feasible to use more than one individual of this species at a time, as the smaller black-phased fishes usually fight violently, as has been noted by Breder (1946). The individual lived in the experimental aquarium until October 2, when it was placed in a concrete outdoor tank, 9 x 6 x 3 feet deep, the interior of which was dark with various sessile growths. By this time the fish had attained a length of 54 mm.

In the experimental aquarium this *Chaetodipterus* behaved in a manner consistent with the observations of Breder and Rasquin (1955), unlike the responses of the species used to check out the operational characteristics of the device. Table IV gives incident light intensity measurements of the light over the aquarium and its reflected values from the bottom. These include reflected values augmented by light under the aquarium to provide values sufficient to give "albedos" unobtainable by simple reflection. The readings showing the fish to be in a banded state are more numerous because when the fish obliterated its bars, by blackening the spaces between them and thus showing a solid black, that particular observation was concluded. Text-fig. 6 shows this data in graphic form and indicates clearly that in all readings of under 300 f.c., the fish was banded and that there were no bars at values above 150 f.c. The pigmentary behavior in the area of transition was not definable precisely. It showed cases that were unstable, the fish varying its pigment alternately, making an arbitrary "barred" or "black" designation impossible.

In the large concrete tank the fish maintained a barred phase, except for the following instances. By October 8, the fish had definitely taken up residence in a hollow cement building block which had been placed on its side and was well covered with dark growths. The fish apparently left this retreat only at feeding times, when the fish became decidedly darker, but did not completely obliterate the pattern of bars. The water ranged between 77° F and 74° F during this period.

When the incoming water began to become decidedly turbid, owing to some nearby dredging operations, the fish no longer darkened at feeding times, but showed its strongest barred black-and-white pattern. Because of the turbidity, the water flow was turned off and the water cleared. This took about five days at the end of which time the water was crystal clear. The fish then showed a solid black pattern on emerging from

its retreat and changed relatively slowly to a barred pattern. By comparison, the clarity of water before the turbidity occurred was only moderate. Under the conditions of the very clear water, when in the retreat, the fish could only see the very dark walls of the tank, which had not been visible to it during the period of turbid water.

When the fish was returned to flowing water and a turbid condition, the black phase completely disappeared. By this time (December 10) the water temperature had dropped to a range of from 72° F to 75° F. Also the days were becoming noticeably shorter and the sunlight weaker. At temperatures below 70° F, this species apparently cannot effectively concentrate the melanin granules. With water temperatures in the sixties, this fish remained darker than in the higher temperature range, but did not become completely black. The low light values evidently permitted a large loss of the many melanophores necessary to permit a black-phased fish.

DISCUSSION

The presence of heavy black pigmentation is common to a considerable variety of acanthopterygians, especially in the young stages, but reports of it occurring in other teleosts are nearly

Table IV.
REACTIONS OF *Chaetodipterus* TO VARIOUS
EXPERIMENTAL LIGHT CONDITIONS

Foot-Candles ¹	Albedo	State of fish
375		
150	0.40	Black
7.5		
2.7	0.36	Banded
30.2		
30.2	1.00 ²	Banded
150		
150	1.00 ²	Banded
300		
150	0.50	Black
355		
22.5	0.06	Black
6.0		
1.1	0.18	Banded
4.5		
0.9	0.20	Banded
2.5		
4.5	0.20	Banded
0 ³		
0	0	Banded

¹Upper figure = Light over aquarium. Lower figure = Light under aquarium.

²Impossible albedos produced by artificial means. See text for details.

³Zero values at night, below threshold of F.C. meter.

all confined to black-phased individuals not found against a light background. Associated with this pigment density, as seen against a light background, are changes in the social attitudes, locomotor behavior, and avoidance reactions.

Since this study is confined to nearly uniformly black fishes, found on light backgrounds in very characteristic solitary and sedentary states, the following comments are given here to avoid possible confusion. Various dark colored fishes not considered here have been excluded for a variety of reasons. These, though apparently few in number, may be illustrated by the following case.

Melichthys radula (Solander) as seen in the sea is a nearly black fish which occurs in aggregations, schools, or as solitary individuals, and is a remarkably fast swimmer for its type, being comparable with the generally gray *Canthidermis sufflamen* (Mitchill), with which it is sympatric. The former, although superficially suggestive of the fishes under consideration, has the following distinguishing characteristics. Although very dark, almost black, there is a brilliant iridescent blue and very narrow line running along the bases of the dorsal and anal fins. There is little pigmentary change in these fishes, but there is a tendency toward yellowish color in their dark sides. This is most pronounced in old aquarium inmates that are not in full health, when the striking blue line fades to whitish. It is doubtful that this species has much color matching ability, which lack is characteristic of the adults of the Balistidae as a whole. However many of the species — especially those that stay close to coral growths — have very gaudy markings of bright colors. That tendency is of course present in most groups of fishes with representatives in such areas.

Environmental circumstances

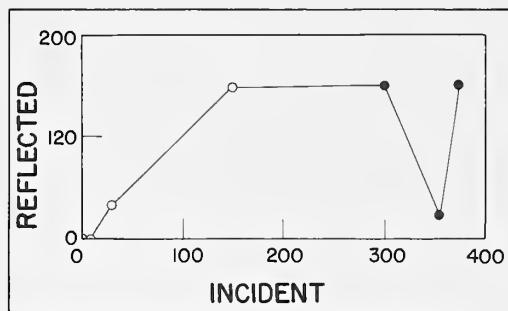
Fishes with a normal melanism are characteristically found either against a black or nearly black background or against a light and strongly contrasting background. The first, which represents the classic matching response is by far the most frequently seen. The first may be shown at practically any size, but the second, so far as known, is mostly limited to the very young or at least the not fully mature fishes. Both background matching and background contrasting fishes can attain almost complete visual obliteration, and for very different reasons. Thus the physical appearance of the background must be of a fairly definite kind in order to enable either of the above pigmentary types to attain any considerable degree of inconspicuousness.

The pattern of backgrounds

Natural backgrounds usually partake of considerable randomness. At this point, however, a consideration of formal geometrical background patterns may be more useful. Obviously at opposite extremes, one could have a pure white and a solid black background. A series of graded gray fields could bridge the two extremes, in as small steps as required. However, all these fields are unlike most natural backgrounds. The grains of pigment making up the lightest gray to the black fields could be enlarged to any size, so that some of the intermediate fields would show polka dot patterns. These could be constructed as black dots on white, or vice versa. Such a pattern of black dots would end in solid black simply by increasing the number of dots per given area. The size of the dots used would determine how fast the fields converged to solid black. It is obvious that some of the intermediate fields would begin to take on a resemblance to light sandy shores with various amounts of dark debris scattered about. Also, it is clear that a stray spot of appropriate size could easily "get lost" on such a field, and even more easily if the backgrounds were randomly distributed instead of being arranged in a precise pattern, and especially so if they were not all perfect circles. Recent studies by Donderi (1966) on the disappearance of identical or similar objects of simplified visual stimulus against a plain background give additional reasons for the effectiveness of this general means of visibility reduction.

Of course, in a natural state, a light colored fish on a light field or a dark fish on a dark field has its visibility greatly reduced. It is in these areas that the adjustable chromatophores evidently operate. It is noteworthy in this connection that many fishes, in or out of a school, are very reluctant to move over a dark patch when in a light phase and vice versa. In clear water it is easy to see such fishes winding their way over a mottled bottom in accordance with this reluctance (Breder and Rasquin, 1951).

Natural sea floors often present a pattern of rather random uniformity for considerable stretches. That is, a fine sand bottom may be considered as a degenerate form of pattern and a smooth unpatterned surface. If the grain particles are increased in size, a coarser pattern develops. It passes through large gravel to boulders and reaches a point where a single large rock covers the area of observation. This, if uniform itself, is again a degenerate pattern. However if this rock has texture, it can be considered in another series. Usually in nature the situation is not so simple but more likely to be



TEXT-FIG. 6. *Chaetodipterus*. Relationship of pigmentation of a single fish to incident and reflected light intensity in foot candles. Black circles indicate the black phase. Light circles indicate the banded phase. Three values for the banded phase, crowded near the origin, are not shown. Based on data of Table IV. See text for full explanation.

a mixed background of two or more separate series in which one, at least, is a near-degenerate pattern and at least one of the others, a rather coarse pattern. Such a case would be a sea floor of fine sand on which rocks of a limited size range are scattered and on which may be a patterning of a limited variety of sea growths. This type of combination of a degenerate background of virtually no pattern combined with a scattering of discrete larger objects is the type in which the black fish phenomenon is most likely to be found. Naturally the discrete objects need not be rocks, but may be anything that locomotion or wave action may distribute in a scattered pattern. Obviously the manner in which these items are scattered insures a certain amount of regularity in both size and shape. This applies to such things as mollusks, sponges, dead leaves, or whatever happens to be common in the locality.

Given a fish of a certain size with reference to the texture of such a background, it is evident that there is an opportunity for a variety of concealing responses, each with its accompanying appropriate behavior. Thus, some fishes match the light sand and avoid the coarse and contrasting darker objects, while others take on darker colors and avoid the light sand background. Also, those that are the subject of this paper, which have darker colors, remain nearly stationary on the light background and become, in effect, just other random objects.

At this point the question of whether a fish matches or contrasts with its background begins to break down and it is seen that one cannot clearly say which is which, however convenient it is to think of light-and-dark-phased fishes in such terms. What can be said, however, is that the light fish has only one way to become inconspicuous; that is to keep in the light phase most nearly matching the sand, whether it is active or stationary, whereas the dark fish has, in theory at least, two choices. These are, of course, settling on the dark objects or settling away from them, but in the latter case remaining relatively quiescent and avoiding association with others and the attending activity and conspicuousness a group entails.⁸ If the question is raised as to why the light colored fish cannot inversely "get lost" on a large dark area with light spots, the answer seems to be that such cases have not been found. Probably the real reason might well be associated with the fact that dark sandy beaches strewn with light colored objects are not easily found. Even if these do occur, they would seem to be altogether too uncommon to make it likely for fishes to adapt to a thing of such limited utility.

It is as yet impossible to say just why these dark fishes usually station themselves about equidistant between dark objects and much less frequently, rest relatively near them. Were it not for this, it would be tempting to imagine that they distribute themselves randomly with respect to the scattering of objects. This would be as much as saying that the fishes are reacting to the randomness of the field, which could not be as effective as if they spaced themselves definitely in respect to the objects in their immediate area, as they evidently do.

The above remarks rest on the idea of specific approach or withdrawal by a fish toward or away from some feature of the bottom or some floating object. Pigmentation adjustment is also a matter of the approach-withdrawal scheme, but on another level, that of the melanin granules within the melanophores, toward or away from each other. In turn these granules invoke accordingly the pale or the dark phase. Therefore, these matters could be considered in the terms used by Schneirla (1959) in the most recent and broadest exposition of his theory of biphasic processes.

The influence of turbidity

Only in very clear water, or in water so shallow that a slight turbidity does not matter, are

⁸ Those dark fish which form groups under such conditions are either highly motile or mimic some objects in the environment, so far as known.

such fishes with contrary pigmentation to be found. One way to change such pigmentation is to turbidify the water (Breder and Rasquin, 1955).

Sometimes one may find that fishes in a light phase and those in a black phase are living in a common area. Breder (1946) reported that *Chaetodipterus* in the black phase was found in two inches or less of water and slightly larger ones, in schools of light phased (banded) fishes, nearby in a foot or more, where the water was sufficiently deep to provide an appreciable turbidity. *Lagodon* is reported performing in a similar manner herein.

Temperature and pressure

In general, organisms with melanophores disperse the granules within them under the influence of relatively low temperatures and concentrate the granules under high temperatures. This is also true of relative pressures and therefore depths of water over organisms. There are some complications to this general statement, involving various species, including some teleosts, as Parker (1948) and Fingerman (1963) have indicated.

It has been argued and in some cases demonstrated with other material that this melanophore activity is thermoregulatory. It is true that dark objects under illumination become heated more than do white ones in identical conditions, but only if not submerged. Because of the heat capacity of water this is not true in aquatic environments, as has been pointed out by Bauer (1941). Moreover even if the above were not true, this situation could hardly function as a thermoregulator as it is "aimed" in the wrong direction to benefit the fishes discussed here, which are not far from their upper thermal limits. What other function such a black investment could have, except as a protection against over-exposure to radiation, is not evident.⁹ While it is true that the phenomenon does not occur in turbid water, it also happens that the species considered have a good development of guanine deposits. Other species without the black covering live in the same environment. They have

elaborate patterns of many sorts or are simply silvery or partly transparent. (See Breder, 1962b, for a discussion of the role of transparency, guanine, and pigment in the mostly transparent planktonic fish eggs and larvae.)

Influences encouraging melanism

It has been demonstrated that a distinct dark phase can be induced experimentally by a number of diverse stimuli and that local darkening can also be induced by suitable local treatment. Extensive references and details may be found in Parker (1948). Other pertinent references follow: Chavin (1956 and 1959), Egami *et al.* (1962), Ellenger (1939 and 1940), Fingerman (1927 and 1930), Fukui (1927 and 1930), Hu and Chavin (1956), Kosto *et al.* (1959), Muzlera (1934), Osterhage (1932), Rasquin (1946 and 1958), Smith, D. C. (1928), and Smith, G. M. (1931, 1932a, and 1932b).

General All-Over Darkening.

1. Internal and external applications of various hormonal and chemical agents, including intermedin, prolactin, MSH, acetylcholine, curare, yohimbine, ethyl alcohol, novocaine, and sodium chloride.
2. Blinding, as by nerve section or opaque eye covers, in the presence of light.
3. Exhaustion from stress, as in an "Omega" fish.
4. Exposure to chill.
5. Exposure to a very dark background.

Localized Darkening.

6. Local applications of hormonal and chemical agents, as listed under item 1.
7. Trauma involving cut cutaneous nerves and severed capillaries, with darkening appearing posterior to the cut.
8. Trauma from radiation with X-rays and cautery, with the darkening variously localized.

This list indicates that, in all but item 5, definitely traumatic or stressful situations are involved. It is not to be inferred that all these methods produce as intense a melanization as may item 5. In fact there is only one method known that will regularly produce a darkening equivalent to that induced by background. This method, item 2, simply eliminates the sense by which the nervous control of melanophores is mediated. Since the fishes of item 5 are obviously not blind, showing normal responses to purely optical stimuli, the importance of the controlling role of vision in their observed reactions is clearly demonstrated.

Two types of activity take place in the case of a fish going into a darker phase. The first is

⁹It is noted that the black investment of abyssal fishes is at the opposite end of the series, being associated with very cold water and the absence of solar radiation. Also at these depths the pressures verge on those inhibiting the concentration of melanin granules, at least of the type possessed by some shallow water species, Marsland (1940, 1942a, and 1942b). Also from the preceding reasons alone, it is doubtful that the discussion between Cowles (1967) and Hamilton and Heppner (1967) could have any direct bearing on the present problem, especially as their work involves only homiothermal terrestrial forms.

the dispersion of granules of melanin in the existing melanophores, the so-called physiological changes. This can happen in minutes or seconds and darkens the fish in proportion to the number of integumentary melanophores present. The extent of the darkening by this means varies with both the species and the individual involved and its recent past history. The second type of darkening is brought about by the development of more melanophores, a process that may run into weeks for completion, the so-called morphological changes. It is, of course, the presence of vast numbers of melanophores that alone can produce the intense blackening considered here. Fishes returning to a lighter phase can at first only lighten their blackness to the extent that the remaining numbers of melanophores will permit. This may not even be noticeable, if their number is so great that even with the greatest concentration of melanin granules, no paler fish results. Therefore the ability to show a changeable pattern likewise must await a reduction of melanophores to a sufficiently low level, which too can take weeks.

Physiological circumstances

Fishes with a sufficiently dense investment of melanophores to be referred to as melanistic are very striking objects when seen against other than a black background or a mottled one of very specific characteristics. These mottlings must bear a relationship to the size of the fish in such a manner that the fish becomes effectively a part of the pattern. One of the most striking features of these fishes is their complete lack of countershading, which is a feature of most non-melanistic fishes and which is important to their ability to become inconspicuous.

Vision and pigment

Most small fishes are not known to produce an intense darkening, even if kept for a long time on a dark background, although in time they reach a dark stage which is evidently as far as they are able to go in this direction. However, this falls far short of the extremes seen in the special cases considered here. When such fishes are placed on a light background they simply revert to an appropriately light phase, apparently as rapidly as their physiological processes will permit. The case of response to a dark spot which has been discussed earlier indicates merely that the reactions differ from those of the black fish in various details.

The case of *Gambusia* in passing from a dark environment to a light one, by natural means (described by Breder, 1947), appears pertinent in this connection. While the fishes immediately

hide under a leaf or similar shelter until they have become sufficiently lightened, there is no evidence of posturing nor need for such behavior under a leaf. In cases where no leaves or other shelters are present, they merely "hug" the walls, as do background-matching fishes when first introduced into a new environment. All this does indicate, however, that fishes on a "wrong" background ordinarily make suitable adjustments in their behavior. The adjustments presumably have considerable protective value. Breder and Rasquin (1951) reported that *Cyprinodon* in a white bucket would hesitate to leave it if lowered into a dark-walled tank. If forced out into such a tank and if it contained larger predatory fishes, the *Cyprinodon* would immediately return to the bucket, but in the absence of the predators, they would instead immediately hide as well as they could in the new non-matching surroundings.

The only chromatophores found in the integument of *Chaetodipterus* are melanophores and a much smaller number of xanthophores. Associated with these pigment bearing cells is a large number of guanine containing cells. Of these the iridophores are numerous and many occur in association with melanophores in the form melaniridosomes. Otherwise there is enough to account for the silvery sheen of these fishes when in their lightest phase. No leucophores were seen, but it is more than likely that a few may be present or developable by the evocation of a suitable background presented for a long time. This species is thus limited to patterns of black, white, browns, and yellows in various combinations. Meek and Hildebrand (1925) described young *Chaetodipterus* as resembling dead leaves. A considerable number of fishes have been noted to bear more than a passing resemblance to leaves, a subject most recently reviewed by Randall and Randall (1960). This type of mimicry is closely related to that of the melanistic fishes here under discussion.

It might be argued that one could be the precursor of the other, but the order of sequence is not clear. Randall and Randall include *Trachinotus falcatus* and *Lobotes surinamensis* in their list of apparent leaf mimics. The adult of the latter species is often very dark or solid black and is commonly found solitary, drifting in the open sea accompanying a log or other object (see Breder, 1949b). Except for *Platax*, other species of young fish resembling leaves are not known to have black adults.

Circadian rhythms

Apparently no studies have been made to attempt to separate the effects of the absence

of light on teleosts from a possible diurnal rhythm which may exist, at least for a time, under constant darkness or illumination. Many teleosts alter their patterns in darkness, usually by concentrating the granules in the melanophores or other pigment cells, *e.g.*, *Holocentrus*, a genus of mostly reddish fishes, which at night are blanched to almost complete whiteness.

Young (1935) described a daily color rhythm in which the cyclostome, *Lampetra*, becomes pale during the night and darkens during the day. He found it responsive to light, but also found a daily rhythm which in some individuals continued for many days when kept in darkness, but for a shorter time than in an alternating cycle of light and darkness. It would be instructive to determine how much of the effect is owed to the direct action of light and how much is endogenous. It may be assumed that various groups of fishes would differ widely in this respect.

Internal secretions

In the literature on the control of chromatophores and color changes, there is little about contrasting pigmentation and where it is mentioned it is usually treated as an unexplained oddity. (See, for example, Parker, 1948, and Fingerman, 1963.)

Enami (1940) found that *Parasilurus asotus* (Linnaeus) darkened on the injection of epinephrin. This is contrary to epinephrin's effects on most other teleosts, but similar to what Breder and Rasquin (1950 and 1955) reported for *Chaetodipterus faber*. They noted that under the influence of this hormone the integumentary melanophores dispersed their granules. However, unlike the effect reported by Enami (1940), the iral and meningeal melanophores, which are part of the epineurial system, concentrated their granules. The fishes described here differed from these injected fishes in that the irises were always found to be as black as the rest of the body.¹⁰

Although it is true that individual species of vertebrates and invertebrates show differing pigmentary reactions to various hormones, there appears to be no reason to suppose that background-contrasting pigmentation has its genesis in peculiarities of the endocrine system, but rather that it is based primarily on the activities of the nervous system under special environmental situations.

¹⁰ The only known exception to this is that of *Trachinotus falcatus*, in which examples in the black phase may have red irises.

Comparison with melanotic conditions

Many fishes have intensely black marks, which are made up of massed assemblages of melanophores, as part of their general pattern. Others show characteristically irregular black marks, which seem to be more or less randomly distributed and may vary widely in number from one individual to another, as in the *Sphyraena barracuda* (Waldbauer) and certain genera of poeciliids, *Poecilia* (*Mollies*), *Gambusia*, and *Xiphophorus* (including *Platypoecilus*). There seems to be no reason to suppose that these are all necessarily precursors to melanomas. However it has been shown, by purely genetic means, that in the case of *Xiphophorus* they could develop into exceedingly virulent melanomas (see, for instance, Gordon, 1948 and 1957).

In addition to the above malignant conditions, a persistent background-developed melanism may be the causative agent in other pathological conditions. Sumner and Douderoff (1938) described an apparently infectious condition associated with lesions and emaciation which occurred in 36% of *Gambusia* kept in black bowls as against 2.5% in white bowls. Thus it would appear that fishes living in a state of continual melanism might be confronted with health problems of a magnitude they would not encounter in an environment incapable of inducing such intense pigmentation. It would seem possible that this circumstance would tend to cause at least some fishes to accept a heavy melanism and therefore a very dark background only as a transient phenomenon.

There appear to be at least three means by which integumentary melanophores can be eliminated by teleosts. Of these one is described by Osborn (1941), in which the degenerating cells and their contents are expelled through the epidermis into the surface mucus and finally washed away. The second is the sloughing off of whole heavily melanistic areas,¹¹ a process which has been described in detail for *Tylosurus raphidoma* (Ranzani) by Breder and Rasquin (1952). Other synentognaths use a third way: *Tylosurus acus* (Lacepede) and two flying fishes of the genus *Cypselurus* simply resorb such areas *in situ* (Breder and Rasquin, 1954). Evidently in the last means of eliminating melanophores and their granules, only phagocytosis is involved. While it is possible that there is also some phagocytic activity present in the other

¹¹ It should be noted in this case that the black area sloughed off is the posterior lobe of the immature dorsal fin and it is accomplished with no evidence of phagocytosis. The black mandibular lappet of this fish is eliminated slightly earlier by simple resorption.

two, it is not yet established and may be slight or absent.

Breder and Rasquin (1952) considered the appearance of the sloughing dorsal lobe of *Tylosurus raphidoma* similar to the second stage of melanosis in *Xiphophorus*, as described by Reed and Gordon (1931). Whether such overextended tissues should be considered benign or simply self-limiting has been discussed by Breder (1952). The latter could conceivably be brought about because of some resulting structural weakness.

Survival values

The contents of the preceding pages suggest that the apparently inverse reactions to light backgrounds can come about only under special and somewhat unusual conditions and that it is possible only in a rather limited variety of fishes. It would appear that fishes which have already abandoned general direct tonal response to a generalized background in favor of colors and general appearances of leaves might take a further step. The further step, that of blackening and appropriately distributing themselves, brings them to the condition discussed here. They have attained an approach to various more generalized but individuated items to which they bear a somewhat general resemblance. There is however no precise matching, such as they may have originally had to leaves of specific plants or trees, but the results must still be of sufficient survival value to be maintained, even if only for certain definite periods in life history.

As earlier suggested it seems to be equally possible that a general blackening provided some early survival value which then went on to a very detailed matching of leaves of a single plant species. There is still insufficient data on this to warrant further speculation on which process would seem the more likely. It might even be that some fishes evolved in one of the above manners while others evolved in the alternate.

The melanophore system of many fishes reacts to the intensity of light by dispersing the melanin granules and to the tone of the background by modulating this behavior, with the result that the fishes approximate a tone similar to that of the background. These two activities have been referred to as the "primary response" for the first and as the "secondary response" for the second. They appear in that order in ontogeny (Parker, 1948). These features of chromatic adjustment are regulated jointly by the endocrine and nervous systems. The endocrine system is in general responsible for the dispersion of the granules and the resulting darkening of the fish, while the nervous system

is similarly responsible for the concentration of granules and the lightening of the fish.¹²

It is the operation of these systems in certain fishes, in shallow strongly illuminated waters, that leads rather unexpectedly to melanization of marked intensity. Similar-appearing melanization is also to be found under the great hydrostatic pressures found in ocean depths. Otherwise the two systems, hormonal and neural, permit the showing of colors and patterns difficult to distinguish from the background. Were it not for the nervous control, mediated through the eyes, fishes would be expected to show their darkest phase under intense light, irrespective of background.

From the preceding it follows that a fish which had been reacting normally to a light background could hardly be expected to change the direction of its pigmentary responses. There appears to be no environmental situation nor physiological condition, in normal feral fishes that could bring this change about. Therefore one is left with the alternative that these fishes in the black phase must have initially adjusted the melanophore system to a very dark or black background. It is possible to establish several observable conditions which suggest just such a genesis of the melanism under study, as follows.

1. Fishes in such a black state are frequently found amid drifting fragments of wood that have been charred or otherwise blackened, and are either floating at the surface or water-logged and resting lightly on the bottom.¹³ All the fishes showing melanism against a light background discussed here hatch from pelagic eggs and spend their larval and sometimes post-larval life as plankton. Therefore such association with small black objects is not especially unusual. In the planktonic environment of the open sea, there is little else to which a chromatically active young fish, with perhaps only melanophores as yet developed, could react. At the place where small black *Chaetodipterus* are most abundant (Text-fig. 4), huge quantities of charred wood fragments often are caught up and swirled about by the same currents which evidently concentrate the black fishes at that place. As these

¹² It is recognized that this is somewhat of an oversimplification, that pigment control is a very complex matter, and that all fishes do not respond in identical fashion. See Odiorne (1957) for a brief summary of these complexities.

¹³ Incidentally there are many more bits of blackened wood floating in the sea than is generally supposed. These bits are naturally most abundant over the continental shelves. They are delivered to the sea primarily by rivers and secondarily by high winds accompanying forest fires or other fires of large magnitude. This material is almost always a uniform dull black and remains buoyant for a long time.

larvae develop and drift into shallow water they drop out of their planktonic stage and take up a more or less littoral bottom life leading to adulthood.

2. If the small fishes are not blackened by means mentioned in item 1, there is added possibility that the young fish on abandoning pelagic life may encounter a sea bottom, or more likely a bay bottom, which is black or at least very dark. Such are not uncommon on the North American Atlantic and Gulf shores. These black items and black-bottom bays are very common where the *Chaetodipterus* studies were undertaken.

3. Whether the black-phased fishes come out of this condition rapidly or very slowly, on encountering a light bottom, is obviously primarily controlled by the density of the melanophores. If the fish has been on a dark background long enough to produce the maximum quantity possible, it may take as long as three weeks for the fish to lighten noticeably. If it had lived on the black background only the minimum time necessary to prevent it from showing a prompt "physiological" change to a lighter and patterned appearance, a sufficient reduction of the melanism to permit such changes would take much less time. A similar appearance would be apparent to the observer, depending on how long ago the fish had left the black background.

That this is not a matter of habituation and a reluctance to change from a quiescent and solitary attitude to an active and social one is indicated by the prompt return to the latter when the pigment has sufficiently lightened. Further elucidation at this time of the relationship between pigment control and social behavior, both of which are chiefly mediated through the eyes in these fishes, would probably have to involve a very difficult differentiation of the precise neural pathways of both actions.

A problem related to the above and to several of the preceding items involves a question of what, if any, influence the early development of abundant melanophores has on subsequent pigment behavior. It is conceivable that such early darkening might induce a bias toward its retention, which could suggest some form of habituation. There is, as yet, no evidence indicative of this, but the presence of such a bias could be readily masked. The thought cannot be summarily dismissed. In three genera the sizes at the onset of heavy melanism are known. None of these genera, *Trachinotus*, *Menticirrhus*, and *Chaetodipterus*, have young which are readily obtained alive or easily maintained under laboratory conditions. Because of this an early solution of the question would seem unlikely.

The preceding three items are all that are necessary to give a plausible explanation of what first appears to be a reverse reaction to the background. The only item that the above does not cover is that of the locomotor behavior and posturing. This is clearly related, however, to the attitudes of other fishes when confronted with a background to which they contrast instead of approximate.

On this basis then, the implications to protective behavior and survival would seem to be clear. The action of the fish thus becomes one of matching the background if possible, but if not, of freezing and arranging itself against a mostly contrasting background as inconspicuously as possible. This action permits time for the slow acting "morphological" adjustments to be made.

Ancillary observations indicate that the black fish phenomenon is a very late spring and summer matter, reaching its full development in July and August and disappearing rather rapidly in the fall, at least in the area in which these studies were made. This is probably no coincidence, for the young of the year of the species involved are present and the long days of summer illuminate the environment at maximum. The length of day may be even more influential than the greater intensity of light at this season.

It should be noted that in all these black fishes, the normally lighter under parts, the ordinary "counter shading," of fishes matching any but fully black backgrounds, is absent. The ventral areas are as black as the dorsal areas. This condition of melanism in any other than a very dark environment would make the fishes very conspicuous. For the validity of counter shading as a protective mechanism, see Cott (1940).

If the various fishes which show a distinctly black phase against a light background are considered from a phylogenetic standpoint, some suggestive relationships appear. It is still too soon, however, to be certain of the significance of these relationships. A list of the groups involved is shown in Table V. It is based on the most recent phylogenetic scheme for teleosts, which has been proposed by Greenwood *et al.* (1966), and is here followed throughout this discussion. The table shows that the phenomenon is confined to what these authors designate as Division III. Within this all are encompassed by two sub-orders, Acanthopterygii and Paracanthopterygii. The single remaining order, Protacanthopterygii, thus far is without such representatives.

Those species that have been observed resting on a light background, in a black phase,

posed in a more or less coiled position, and lacking the tendency toward hasty departure on approach, represent eight genera as shown in Table V. The other nine genera in which the possibility of the typical black fish reactions seem likely have not been under close observation. These are also indicated in this table. Taken together, the data in Table V indicates that this condition is most strongly represented in the Percoidei, with five and six genera respectively. In the Paracanthopterygii, there are three genera all of which are in the Antennarioidei. The single non-teleost which has been mentioned is the Holostean, *Lepisosteus*. It thus seems likely that this natural melanism may be found to be confined to this single but broad band of phylogeny.

SUMMARY

1. Fishes are discussed which display an almost complete melanism against a light background and which are consequently strongly contrasted to it.
2. The locomotion and social attitudes of these dark fishes are unlike those of individuals of the same species not in the black phase, as the latter aggregate or school and escape capture by fleeing, whereas the black individuals are solitary, quiescent, and agonistic and freeze on approach, usually in a characteristic twisted pose.
3. This phenomenon, so far as known, is confined to young acanthopterygian fishes of the families Carangidae, Sparidae, Sciaenidae, and Ephippidae, although there are suggestions of it in other families of teleosts and one holostean.
4. It has only been found in warm water during the warm half of the year.
5. The species best known to display melanism in this manner are *Trachinotus falcatus* (L.), *Lagodon rhomboides* (L.), *Menticirrhus* 4 sp., and *Chaetodipterus faber* (Br.), with over fifteen other cases, involving species about which there is some uncertainty.
6. The apparent conspicuousness of the black phase, on a light background, is mitigated to a very great extent by the usual scattering of small dark objects, such as tiny shells and bits of decaying plants.
7. This item and all following are interpretations, based on field observations and experiments. The black phase must appear initially from exposure to a dark background, because of the manner in which the neuro-endocrine controls operate.

8. Prompt "physiological" response to displacement to a light background in a bright light is usually impossible because of the intense melanization which requires the slower "morphological" loss of melanophores before the change can become apparent.
9. The length of time a fish retains this melanic condition is dependent on how long it has resided on a dark background and how recently it has left it.

Table V.
PHYLETIC OCCURRENCES OF "BLACK-FISH" BY GENUS AND HIGHER TAXA.

Bold face; definite, by observation. *Italics*; possible or probable, by inference.

Paracanthopterygii	
Lophiiformes	
Antennariidae	
<i>Antennarius</i>	1 ¹
Ogcocephalidae	
<i>Ogcocephalus</i>	1 ¹
Acanthopterygii	
Perciformes	
Percoidei	
Serranidae	
<i>Epinephelus</i>	1 ¹
<i>Mycteroperca</i>	1 ¹
Carangidae	
<i>Trachinotus</i>	1
Lobotidae	
<i>Lobotes</i>	1
Sparidae	
<i>Lagodon</i>	1
Sciaenidae	
<i>Menticirrhus</i>	1 ¹
Ephippidae	
<i>Chaetodipterus</i>	1
<i>Platax</i>	1
Pomacentridae	
<i>Abudefduf</i>	1
Labroidei	
Labridae	
<i>Tautoga</i>	1
<i>Tautogalabrus</i>	1
Blennioidei	
Clinidae	
<i>Stathmonotus</i>	1
Pleuronectiformes	
Soleoidei	
Soleidae	
<i>Gymnochirus</i>	1
Tetraodontiformes	
Balistoidei	
Balistidae	
<i>Monacanthus</i>	1 ¹

¹This genus does or may contain more than one species subject to the "black-fish" phenomenon.

10. The size at which fishes outgrow this type of reaction appears to be related to light intensity as modified by water turbidity.
11. The entire phenomenon may be almost entirely on the ontogenetic level, but apparently in certain cases some is on the phylogenetic level, at least in *Chaetodipterus faber*.

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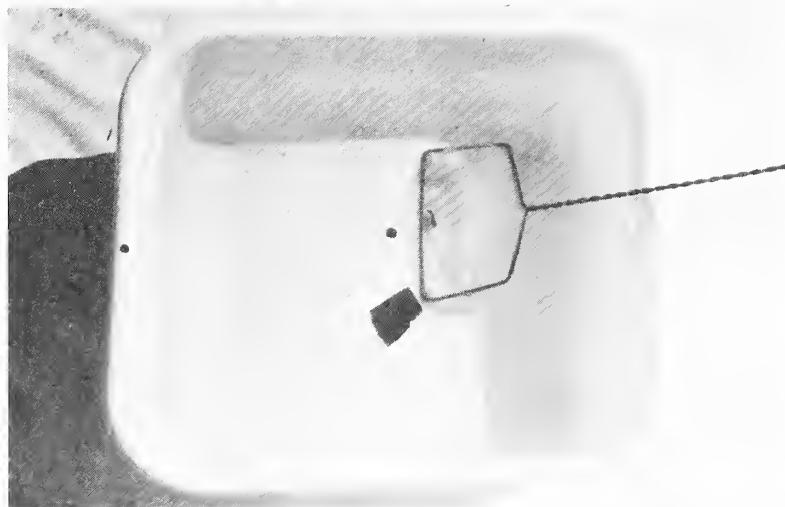
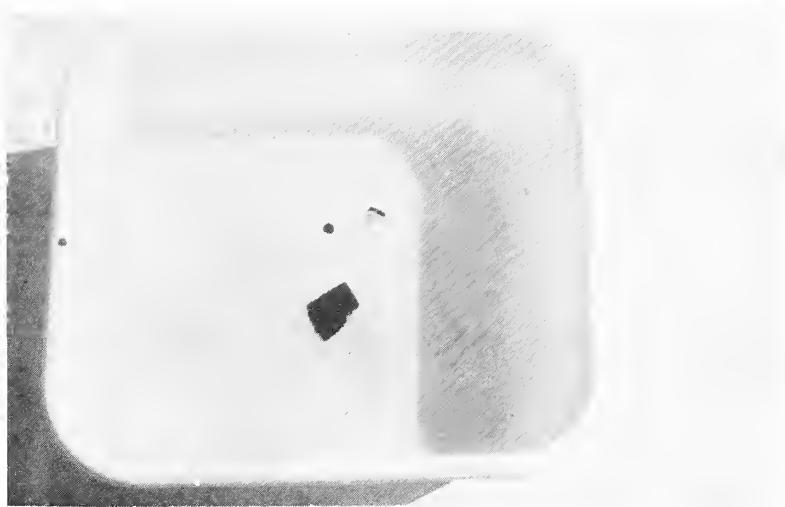
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EXPLANATION OF PLATE

PLATE I

The black phase of *Trachinotus falcatus*. Three views of a single individual confined in a white basin. From top down: a typical posture in reference to two black spots; a net thrust under the fish, indicating its quiescent nature, despite the fact that the net necessarily displaced the fish in order to get under it; fingers thrust astride of the fish and wiggled, the latter activity being responsible for the surface ripples. See text for full explanation.



Color Pattern of the Eastern Pacific Spotted Porpoise *Stenella graffmani* Lönberg (Cetacea, Delphinidae)

WILLIAM F. PERRIN¹

(Plates I-VII; Text-figures 1-3)

Developmental, individual, and between-school variation in coloration is described. Newborn are unspotted, and are dark-gray above and white below. Dark-gray ventral spots appear first at side of jaw and in area ahead of flipper, then develop rapidly over entire ventral surface. Ventral spots fuse in adults to yield uniform gray appearance below. Dorsal light-gray spots begin to develop after appearance of ventral spots and vary greatly in size and density in adults. System of markings about head, including eye patch, eye band, gape border, forward extension of cape mark, and flipper band, reach highest degree of contrast with ground coloration in subadults and persists only faintly in adults. Features that show great individual variation include extent of secondary dark-gray brushings on head of newborn and development of dorsal spotting in adults. Features showing variation between schools include structure of flipper band, definition of cape mark, definition of secondary light-gray band below cape mark, and color of tips of jaws. Coloration is similar to *S. attenuata* except for contrast between components of pattern, but different from that of *S. plagiodon*.

INTRODUCTION

POPOISES of the genus *Stenella* are not only of high scientific interest, but are also important to the multimillion-dollar, California-based tropical tuna fishery. Two porpoises—the spotted *Stenella graffmani* (Lönberg), and a form called “spinner porpoise” by fishermen, assigned to *S. microps* (Gray) by Handley (Hester, Hunter, and Whitney, 1963) and to *S. longirostris* (Gray) by Nelson (1889) and Hershkovitz (1966)—and yellowfin tuna, *Thunnus albacares* (Bonnaterre) occur together in large school complexes in the eastern central Pacific. Fishermen locate the tuna by spotting the porpoise schools at the surface. The association between fish and the porpoise is very close, and the fish schools can be slowed, consolidated, and otherwise directed by herding the porpoise (Inter-American Tropical Tuna Commission, 1968; McNeely, 1961; Perrin, 1968). Despite their economic importance, little is known of the biology of either of the porpoises. The present report describes color pattern development

and color variation within and between schools of *Stenella graffmani*.

Little has been recorded about the coloration of *S. graffmani* since it was described by Lönberg (1934) from a salted skin and part of the skull of a large male collected near Acapulco, Guerrero, Mexico. He described the skin as follows: “The colour of the skin, since the salt had been removed, was coal black all over but with small scattered, whitish-gray spots, chiefly on the back, and perhaps more numerous on the back behind the dorsal fin. On the lower parts of the sides these spots were much less numerous and much smaller in size than those of the back.” His figure of the type-specimen was based on a photograph of the dried skin after it had been partially prepared for mounting. The spotting described by Lönberg is evident in his figure, but a characteristic ground pattern, described below, apparently was obliterated by the salting process.

Hall and Kelson (1959), perhaps following Lönberg’s description, described *S. graffmani* as “blackish throughout, mottled dorsally with grayish-white.” Walker (1964) published a good lateral photograph of what appears to have been

¹Bureau of Commercial Fisheries, Fishery-Oceanography Center, La Jolla, California 92037.

a large adult female. The spotting pattern is easily seen, and some elements of the ground pattern are discernible. Ingles' (1965) wash drawing is inaccurate in shape and coloration. A drawing published by Daugherty (1965) depicts the shape of the animal more accurately but represents the color pattern poorly. She described the pattern as "... uniform gray, with scattered small spots of white or light gray. The spotting is variable, sometimes being quite conspicuous, especially in certain body areas, at other times being hardly noticeable. It is undoubtedly more distinct in live animals than in the dead ones which the tuna boats bring in."

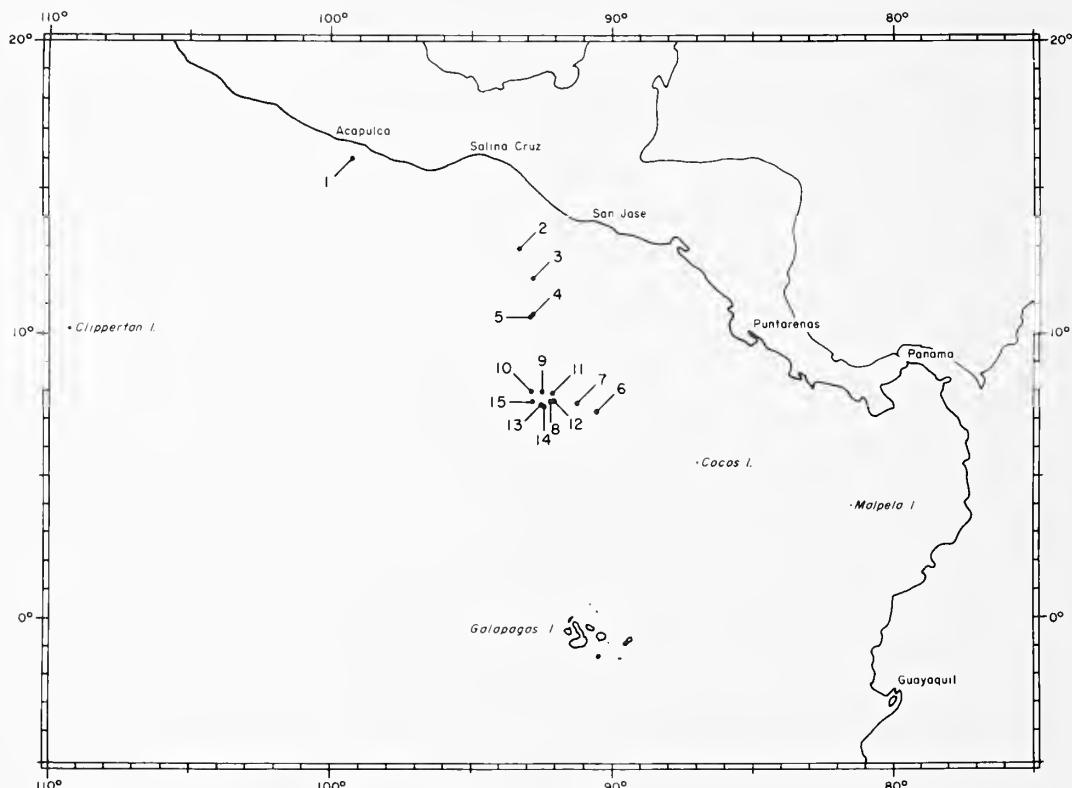
The only previously published observation on the variation of coloration other than in adult specimens of *S. graffmani* is the report by Caldwell and Caldwell (1966) of an unspotted calf taken from the uterus of a spotted mother. As is shown below, this difference is a function of age.

The inadequacy of the record can be laid to the difficulty of obtaining and studying specimens, especially fresh ones, of a tropical pelagic cetacean such as *S. graffmani*. American tuna fishermen have in recent years begun to use very large purse seines in areas where schools of

S. graffmani are closely associated with tuna schools. This circumstance has lately made the species accessible to study.

MATERIALS AND METHODS

This report is based on specimens, notes, and photographs that I collected during a cruise to the eastern central Pacific aboard a commercial tuna seiner, from April 1 to April 29, 1968. Fifteen net sets, numbered 1 to 15 (Text-fig. 1), were made on porpoise from tuna-porpoise associations. Since deck space was required for examination of the animals, the amount of data that I could collect from a particular set depended on the time of day, the amount of fish in the net, and other factors that affected the fishing operation. Extensive observations on large numbers of animals could be made only when the net set was completed at or near the end of the fishing day; it was then possible to keep porpoise on deck until the following morning. Some color observations were made on all 15 of the school samples, and more detailed notes were taken on 129 specimens from four schools. Extensive morphometric and ecological data that were gathered will be reported elsewhere.



TEXT-FIG. 1. Locations of net sets numbers 1-15. *Stenella graffmani* was taken in all sets except no. 14.

The degree of sexual development of 107 animals was estimated by a rapid field examination of the gonads. Males with full-size testes (approximately 30 cm in length) were adjudged mature. The females that were not pregnant or lactating fell into two groups, those in which both ovaries were flat and obviously immature and those in which one or both ovaries were fully developed and contained corpora albicantia or maturing follicles. Since gonads were not examined histologically, the determinations of maturity must be considered estimates.

DEVELOPMENTAL AND INDIVIDUAL VARIATION

When a number of spotted porpoise from a single school are laid on the deck of a ship, the first impression is one of wide variation in coloration. In the schools I examined, however, the animals could be grouped roughly into the following five general categories of color pattern (Pl. I):

a. *Newborn stage*. Dark purplish-gray dorsal surfaces and lateral brushings, with white ventral surfaces and no spots; displayed by the smallest individuals, some of which retained shreds of umbilical cord.

b. *Two-tone stage*. General two-tone pattern with dark-gray surfaces above, lighter-gray lower surfaces, and a well-defined pattern in varying shades of gray about the head and flippers; no spots. The individuals in this and the following two groups were progressively intermediate in size between the smallest (newborn) and largest animals.

c. *Speckled stage*. Same as two-tone but with discrete, very dark-gray spots on the ventral surfaces; discrete light-gray spots on the upper, darker surfaces present on some animals but lacking on others.

d. *Mottled stage*. Ventral spots converging and overlapping in places, but patches of the lighter-gray background still visible, yielding a mottled effect; discrete or merging light-gray spots present on the upper surfaces.

e. *Fused stage*. Ventral spots completely convergent, to give the effect of a uniform, medium-gray to dark-gray surface; on close inspection, the individual overlapping spots still discernible; displayed by the largest individuals.

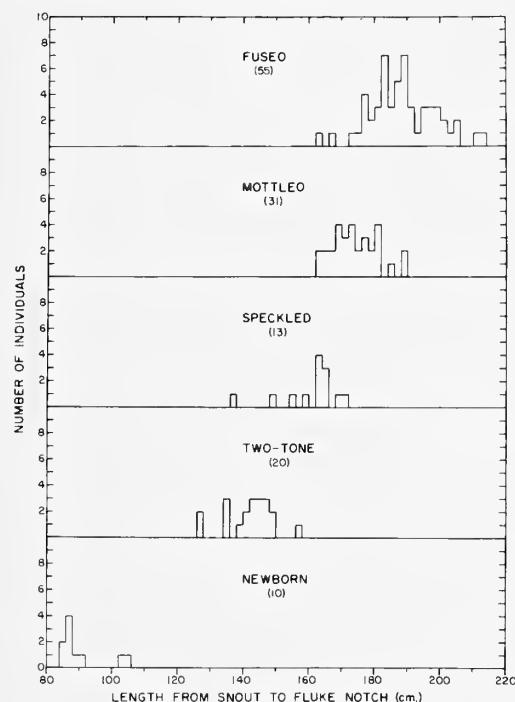
These five categories represent definable increments in a continuous development of coloration. The rather close correlation between these pattern categories and the size of the animals (Text-fig. 2) demonstrates clearly that the primary component of the spotting variation is developmental. An alternative explanation—that size, and therefore spotting development, are

independent of age—is eliminated by data on maturity (Table 1). None of the two-tone or speckled animals were sexually mature; nearly one-third of the mottled animals were mature; and all but one of the fused individuals were mature. This sequence indicates that the onset of sexual maturity occurs during or shortly after the mottled stage.

Color of Newborn Animal

The newborn animal (Pl. II, fig. 2) is dark-gray above and creamy-white below. The boundary of a well-defined mark, referred to below as the cape mark, extends from the apex of the melon, over the eye, to behind the dorsal fin. In the latter area, approximately one-fourth of the distance from the dorsal fin to the flukes, the boundary is less sharply delineated. In lateral view, the cape extends approximately two-thirds of the way down the side of the animal above the anterior insertion of the dorsal fin.

The area from the vertical through the genital region to the flukes is sharply divided along a line that runs forward from the lateral fluke origin into a dark-gray area above and a lighter portion below. The area below the line shades from white above the anus to dark-gray



TEXT-FIG. 2. Relationship between size and development of ventral spotting in 129 specimens of *Stenella graffmani*. Sample size is shown in parentheses.

TABLE 1.

RELATIONSHIP BETWEEN SEXUAL MATURITY AND DEVELOPMENT OF VENTRAL SPOTTING IN 102 SPECIMENS OF *Stenella graffmani*

Color pattern	Males		Females	
	Number examined	Number mature	Number examined	Number mature
Two-tone	12	0	11	0
Speckled	4	0	5	0
Mottled	14	1	10	6
Fused	13	12	33	33

at the fluke origin. The gray of the upper half of the divided area extends forward and into the cape region, but the margin there is more diffuse. A narrow, diffuse streak of the same shade of gray arises from the lower margin of the dark area at approximately above the posterior insertion of the flipper. It extends posteriorly and slightly into the white area below the cape.

Seen from below, the pure white of the lower surface narrows to a line along the ventral keel at about half the distance between the anus and the fluke notch. The white edging extends to the end of the keel.

Coloration about the eye is distinctive. A dark eye patch is drawn out at its forward margin into a narrow eye band which extends forward along the rostral groove and joins the cape mark near the apex of the melon. This well-defined eye marking is overlaid with a more extensive diffuse marking of lighter-gray. There are brushings of the same gray color on the upper side of the snout and on both sides of the lower jaw. Individual variation is great in the width and definition of the eye band and in the extent of the lighter-gray overlaid markings (Pl. II, fig. 3). Animals with extensive brushing around the eye also have a faint suggestion of a broad, very diffuse band extending from the eye region to the flipper origin.

The flippers and flukes are dark-gray on both surfaces, and the dorsal fin is also uniform dark-gray.

Inferred Development of Coloration

As the porpoise increases in size, the entire region below the cape mark darkens to a light-gray (Pl. II, fig. 4). The secondary brushings about the eye and snout are no longer evident. The eye band becomes part of a well-defined system of connected markings (Text-fig. 3) that includes a dark margin around the most posterior part of the gape and the dark flipper band, which extends from the gape to the anterior insertion of the flipper. This pattern persists throughout further development. Anteriorly the lower margins of the flipper bands extend ventrally, becoming confluent in the gular area about four-fifths of the distance from the tip

of the snout to the end of the gape. There is great interschool variation in the extent and delineation of the flipper band (discussed below). Parallel to the margin of the cape mark is a narrow lighter-gray band, approximately as wide as the eye patch (Pl. III, fig. 5). The band disappears approximately below the dorsal fin tip; definition of the band varies among schools.

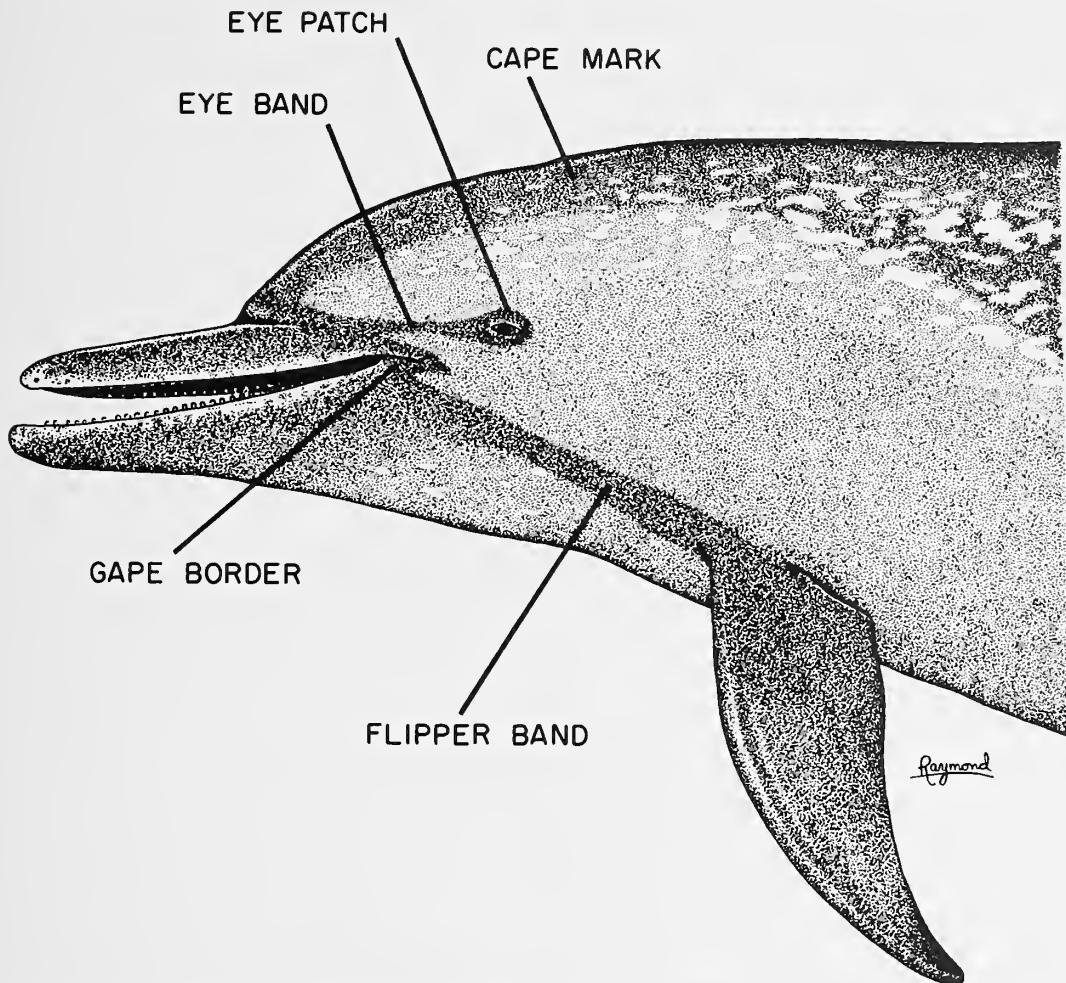
The next event in the developmental sequence is the appearance of dark-gray spots on the ventral surfaces. The spots appear first on the side of the lower jaw and in the flipper band near the anterior insertion of the flipper (Pl. III, fig. 6). They seem to appear rapidly during growth over the entire ventral surface, but remain densest on the mandible and in the flipper band (Pl. IV, fig. 7). The spots become larger and begin to overlap (Pl. V, figs. 8 and 9), and the flipper bands become less evident (Pl. VI, figs. 10 and 11). At this stage, the animal has a mottled appearance below. The spotting may extend to both surfaces of the flippers. Individual variation in regularity of size and spacing of the spots results in variable appearance of the ventral aspect during the mottled stage. As growth proceeds, the spots coalesce least rapidly in the gular and genital regions. When fusion is complete, the spots are no longer clearly evident and the animal appears uniform gray below (Pl. VI, figs. 10 and 11), although the spots may still be detected upon close inspection. The pattern about the head, including the eye band and flipper band, is still apparent, but faint.

After the ventral dark spots have appeared, very light-gray spots become evident on the dark-gray dorsal surfaces (Pl. V, fig. 8). Their size and number rapidly increase, and they become densest and may overlap at the margin of the cape mark above the eye and in the area immediately posterior to the cape mark (Pl. VI, figs. 10 and 11, and Pl. VII, fig. 12). The density of light spots in these areas and over the rest of the upper surfaces, once the fused stage has been reached, varies within a school (Pl. VII, fig. 13) and bears no apparent relationship to the size of the animal. In some individuals, the light spotting extends to the area below the cape mark.

BETWEEN-SCHOOL VARIATION

In addition to the developmental and individual variation within schools, I observed between-school variation in several features:

1. The structure of the flipper band varied between schools from a simple band (Pl. II, fig. 4) to a wider, more complex structure (Pl. III, fig. 6).
2. The narrow light-gray band contiguous to the cape mark was very strongly defined in the subadults of some schools (Pl. III, fig. 5). The



TEXT-FIG. 3. Pattern on head of adult *Stenella graffmani*, with explanation of terms used in text. Sketched from female, 195 cm, from set no. 7.

presence of this band was correlated with a poorly defined upper margin of the flipper band.

3. The contrast between the cape mark and the lighter lower surfaces varied. The larger individuals taken in set number 5 appeared at first sight to be uniform dark-gray with light dorsal spots. Closer inspection, however, revealed a faint cape mark.

4. In some schools, the larger adults had white-tipped jaws (Pl. VII, fig. 14), correlated with a faint light-gray flecking of the dark-gray ventral surface, especially in the gular region.

On the basis of color notes and photographs, I scored each of five schools for each of these four features (Table 2).

Fraser (1966) posed a stimulating question about schools of tropical *Stenella* species. He asked, "Are the dolphins fortuitously congre-

gated for some purpose such as feeding, breeding, or deriving benefit from especially favorable environmental conditions? Or is each school formed by the natural increase of an isolated family unit?" The between-school differences in coloration detected in *S. graffmani* suggest that schools of this species may constitute genetic entities. Between-school variation in skeletal and external morphometric characters has yet to be examined for any of the spotted porpoises.

COMPARISON WITH OTHER FORMS

The developmental sequence in color pattern parallels that described for *Stenella plagiodon* (Cope)² by Caldwell and Caldwell (1966) except that in *S. plagiodon* the ventral dark spots do not become fused. The adults figured by the

² Placed in the synonymy of *S. pernettyi* (Blaineville) by Hershkovitz (1966).

TABLE 2. BETWEEN-SCHOOL VARIATIONS IN COLOR PATTERN OF SPECIMENS OF
Stenella graffmani FROM SIX SCHOOLS

The symbol — indicates feature absent or so poorly defined as to appear absent; + indicates feature present and sufficiently well-defined to be readily observable; ++ indicates feature was strikingly well-defined.

Feature	School (set number) and (in parentheses) number of animals examined					
	4 (33)	5 (31)	8 (92)	9 (183)	11 (34)	12 (48)
1. Complex flipper band	—	—	+	+	+	+
2. Secondary light band below cape	+	—	+	+	—	+
3. Contrast between cape and ground	++	—	+	+	+	+
4. White jaw tips	—	—	+	+	++	—

Caldwells and others (True, 1885; McBride, 1940; Moore, 1953) are all spotted or mottled below. Other differences in pattern are evident from the photographs: In *S. plagiodon* the ventral ground is white rather than light-gray; the lateral and dorsal light spotting is developed to a higher degree; the cape mark is apparently present in the unspotted juvenile but is not evident in the photographs of older, spotted animals; and a light line runs from the eye to the posterior insertion of the flipper in unspotted young specimens (absent in *S. graffmani*).

The coloration of the other common spotted porpoises, *S. attenuata* (Gray)³ in the south Atlantic and central and western Pacific and *S. frontalis* (Cuvier) in the Atlantic, is less well known than that of *S. plagiodon*. Photographs of *S. attenuata* from Japan (Nishiwaki, Nakajima, and Kamiya, 1965) show a cape mark and eye and flipper bands like those of some individuals of *S. graffmani*. In reference to spotting, Nishiwaki *et al.* stated ". . . the dorsal half of the body is blueish purple black with numerous gray and white spots, and the ventral half of the body is gray with numerous tiny white spots. There are no spots on the head, the dorsal fin, the flippers, and the tail flukes." The jaw tips are white. The contrast between the cape mark and the lighter area below appears to be much stronger than in *S. graffmani*. In the specimens of *S. graffmani* that I examined, white jaw tips and white-flecked ventral surfaces were present in some schools, and the degree of light spotting in the dorsal region varied within schools; consequently, the only consistent difference in coloration between the specimens of *S. attenuata* which Nishiwaki *et al.* figured and those of *S. graffmani* described in the present paper is in the degree of contrast between the cape mark and the area below.

Dawbin (1966) published a photograph of six spotted porpoises (heads only) taken by natives on the island of Malaita in the Solomons. He assigned these animals to "the *S. attenuata-frontalis* group." The portion of the color pattern that can be seen corresponds to the pattern in *S. graffmani* in every respect.

A specimen of *S. frontalis* from the coast of French Equatorial Africa that Fraser (1950) described in great detail did not differ in color pattern from *S. graffmani*. The jaw tips were white, and the ventral surface was ". . . dark gray with abundant darker spots and fewer scattered white spots." Fraser cited the fact that Lönnberg's (1934) description of the type of *S. graffmani* did not mention a white snout tip and chin and concluded, "It is only in the flecking on the body that this species can, by color, be connected with the 'Atlantide' specimen — *S. frontalis*." White snout tips, as noted above, occur in some individuals of *S. graffmani*. This feature has now been noted in all the spotted porpoises (Nishiwaki, 1965; Dawbin, 1966; Caldwell and Caldwell, 1966).

Of three spotted porpoises from West Africa that Cadenat (1959) described, one that he tentatively referred to as *S. frontalis* corresponds to *S. graffmani* in coloration. The remaining two more closely resemble the specimens of *S. plagiodon* depicted by Caldwell (1966), and he indeed tentatively referred one of them to that species.

The closely similar or identical color patterns of the nominal species of spotted porpoises point out the need for intensive and standardized observations on large series of these animals. From my observations on *S. graffmani* and from previously published descriptions and figures of color patterns in *S. frontalis* and *S. attenuata*, I see no basis at present for separation of these three forms by coloration. This is not to say that they may not prove to be separable on the basis of other characters.

³ Placed in the synonymy of *S. dubia* (Cuvier) by Hershkovitz (1966).

The conclusions reached here are tentative, because they are based on data for a relatively small number of schools from a restricted portion of the geographical range of the species. Definition of the total range of variation and more accurate delineation of the developmental, individual, and between-school components of variation must await the availability of larger series, from throughout the range.

ACKNOWLEDGMENTS

This study was supported by the Bureau of Commercial Fisheries and the Zoology Department of the University of California at Los Angeles. Kenneth S. Raymond prepared Text-figs. 1, 2, and 3, Pl. I was painted by George M. Mattson. Dr. Kenneth S. Norris and Dr. Carl L. Hubbs read the manuscript and made many helpful suggestions. Collection of the data was made possible through the cooperation and assistance of the owners, captain, and crew of the tuna boat *Carol Virginia*.

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EXPLANATION OF PLATES

PLATE I

- FIG. 1. Development of color pattern in *Stenella graffmani*, showing observable increments described in text: a. newborn, b. two-tone, c. speckled, d. mottled, e. fused. Painted by George M. Mattson from photographs and field notes.

PLATE II

- FIG. 2. Newborn *Stenella graffmani*, female, total length (tip of snout to fluke notch) 87 cm. From set no. 5.
- FIG. 3. Lateral views of heads of four newborn female specimens of *Stenella graffmani* from set no. 5. Lengths from left to right: 85 cm, 85 cm, 87 cm (same animal shown in Fig. 2), 86 cm. Note variation in markings about the eye. In the first three individuals the basic dark eye band is overlaid with a more diffuse and more extensive marking of lighter gray.
- FIG. 4. Subadult *Stenella graffmani* at two-tone stage. Female, 141 cm, from set no. 5. The scattered white flecks are adhering fish scales.

PLATE III

- FIG. 5. *Stenella graffmani* at two-tone stage, showing light band below the cape mark. From set no. 8. Sex and length data for this specimen and for others of those figured below were not gathered. The reason for these gaps in the data is explained in the text.
- FIG. 6. *Stenella graffmani*, showing early stage of ventral spot development. From set no. 11.

PLATE IV

- FIG. 7. Lateral views of head, middle, and tail regions of *Stenella graffmani* at the speckled stage. Female from set no. 11. The white flecks are adhering fish scales.

PLATE V

- FIG. 8. *Stenella graffmani* at mottled stage. Female, 184 cm, from set no. 12.
- FIG. 9. Ventral views of *Stenella graffmani* at early speckled (lower) and mottled stages. Female (lower), 163 cm; and male, 165 cm, from set no. 10.

PLATE VI

- FIG. 10. Adult *Stenella graffmani* at fused stage with light dorsal and lateral spotting. Male, 187 cm, from set no. 12.
- FIG. 11. Ventral views of three adult specimens of *Stenella graffmani* at fused stage, from set no. 9. From bottom: male, 200 cm; female, 183 cm; female, 176 cm.

PLATE VII

- FIG. 12. *Stenella graffmani* with heavy dorsal and lateral spotting. From set no. 10.
- FIG. 13. Sample from one school of *Stenella graffmani* on deck of tuna seiner. Note variation in dorsal and lateral spotting.
- FIG. 14. Large adult *Stenella graffmani*, showing white jaw tips and lips. From set no. 11.

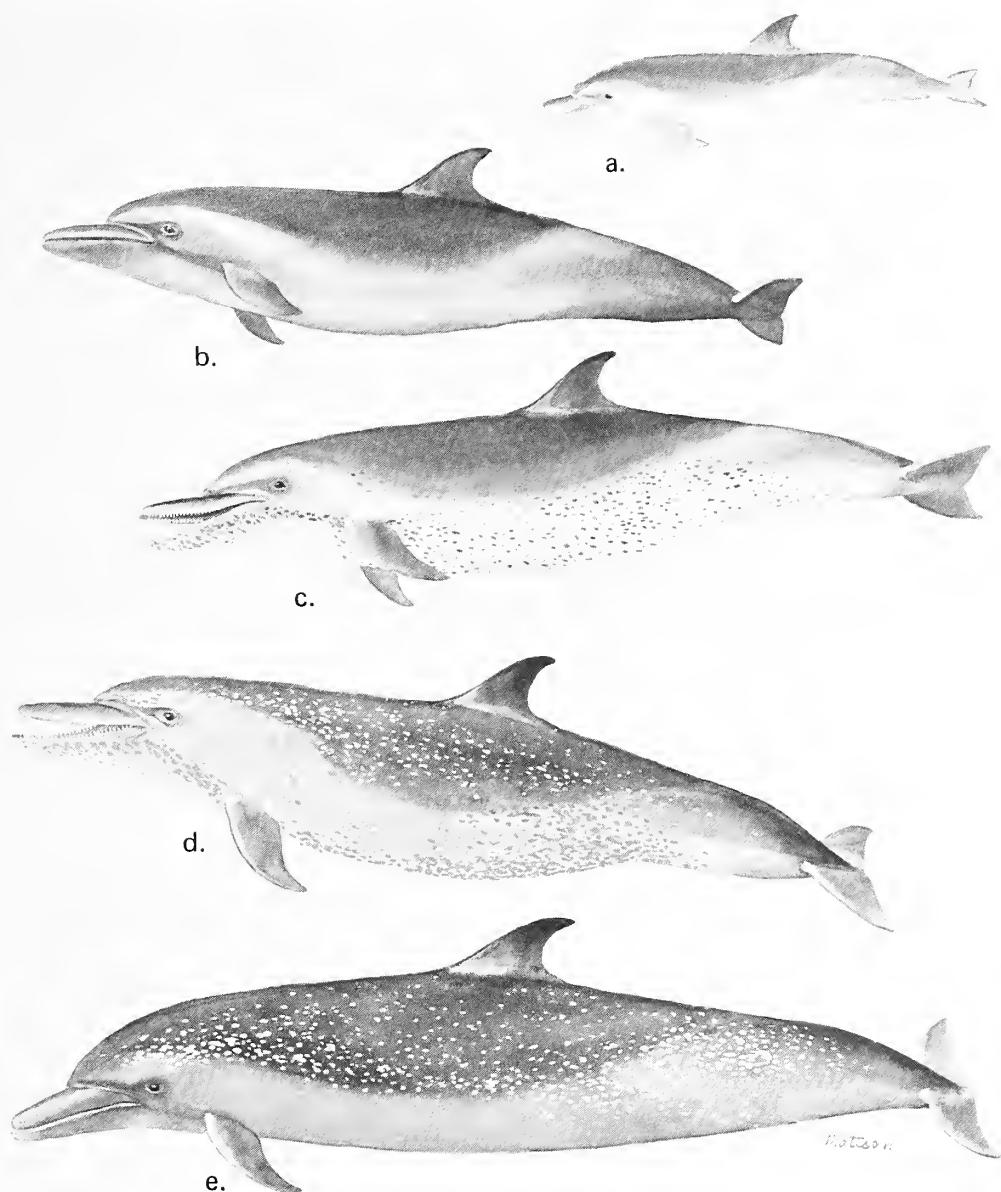
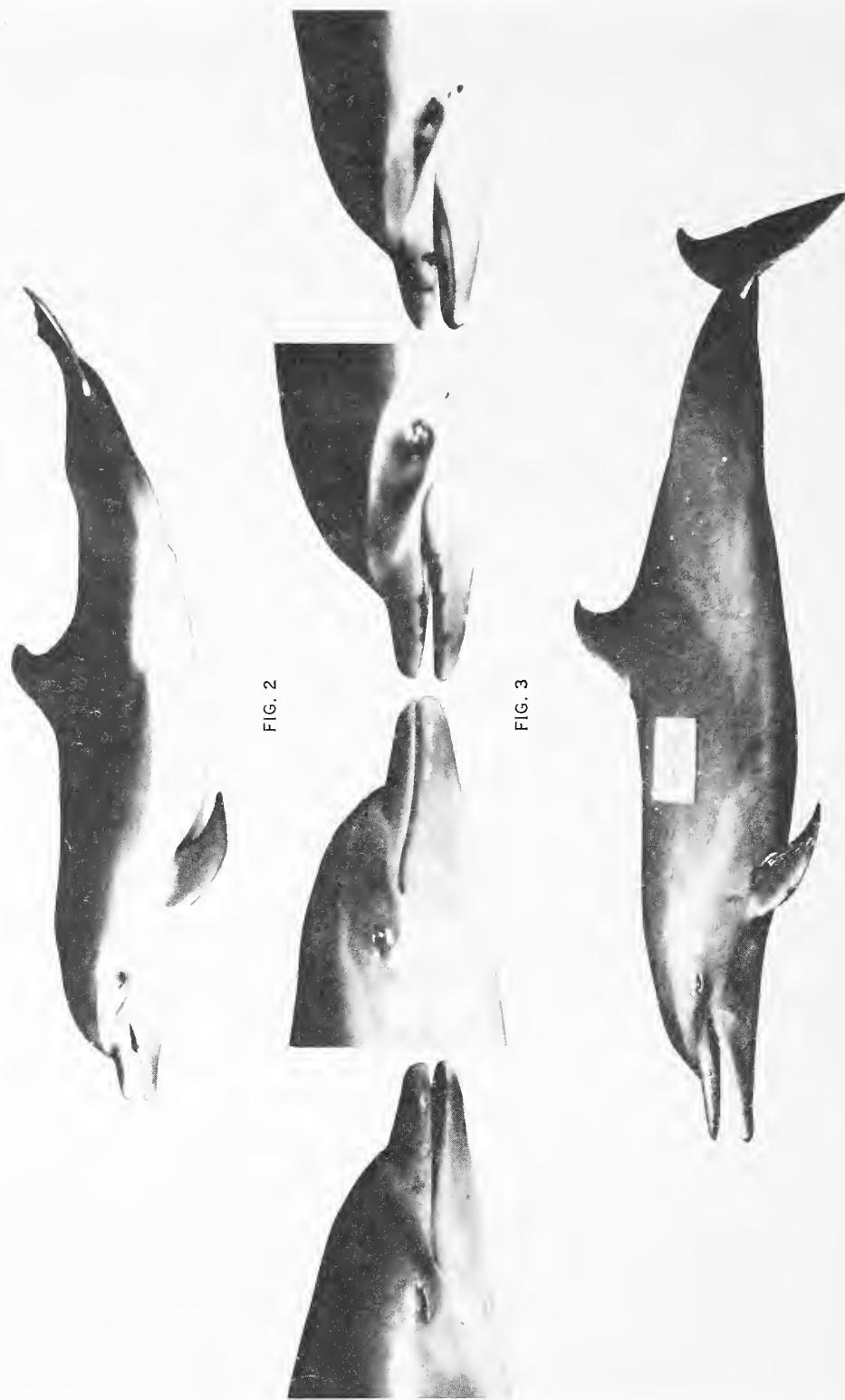


FIG. 1

COLOR PATTERN OF THE EASTERN PACIFIC SPOTTED PORPOISE
STENELLA GRAFFMANI LONNBERG (CETACEA, DELPHINIDAE)



COLOR PATTERN OF THE EASTERN PACIFIC SPOTTED PORPOISE
STENELLA GRAFFMANI LONNBERG (CETACEA, DELPHINIDAE)

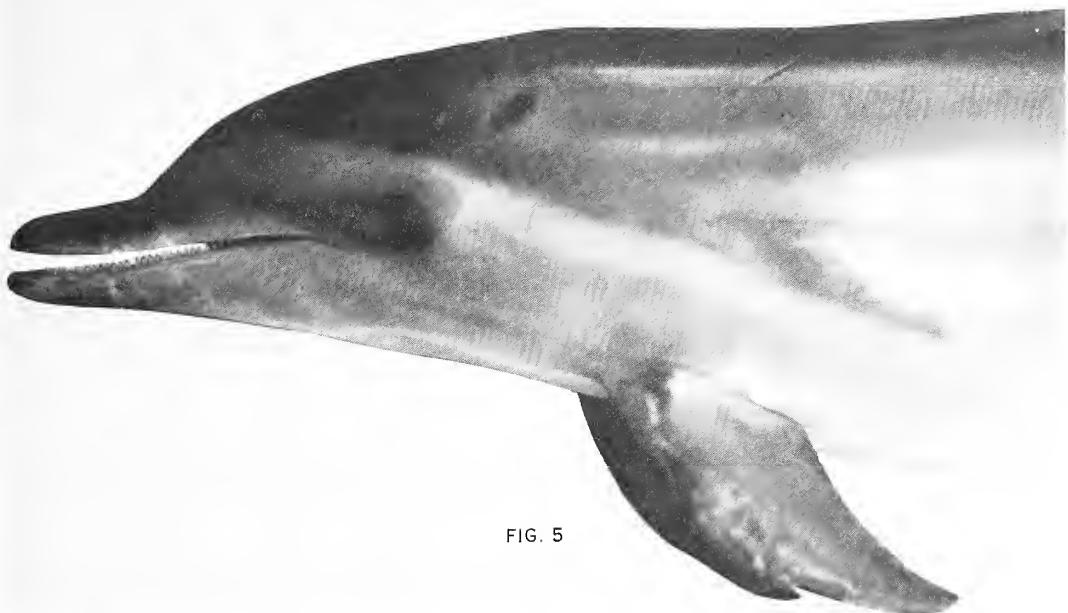


FIG. 5



FIG. 6

COLOR PATTERN OF THE EASTERN PACIFIC SPOTTED PORPOISE
STENELLA GRAFFMANI LONNBERG (CETACEA, DELPHINIDAE)



FIG. 7

COLOR PATTERN OF THE EASTERN PACIFIC SPOTTED PORPOISE
STENELLA GRAFFMANI LONNBERG (CETACEA, DELPHINIDAE)

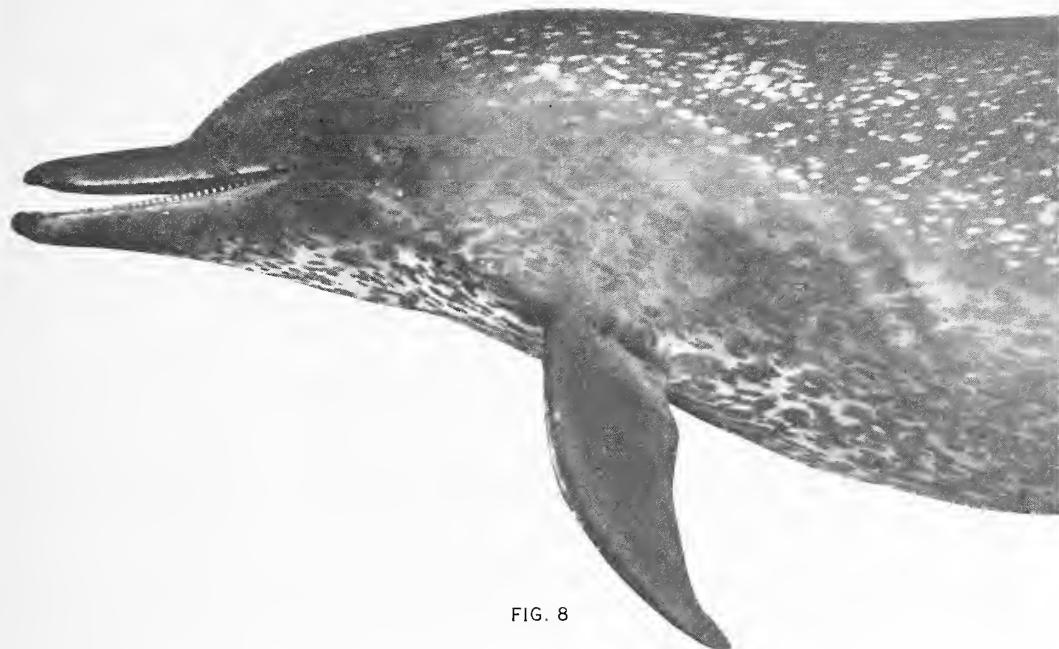


FIG. 8



FIG. 9

COLOR PATTERN OF THE EASTERN PACIFIC SPOTTED PORPOISE
STENELLA GRAFFMANI LONNBERG (CETACEA, DELPHINIDAE)

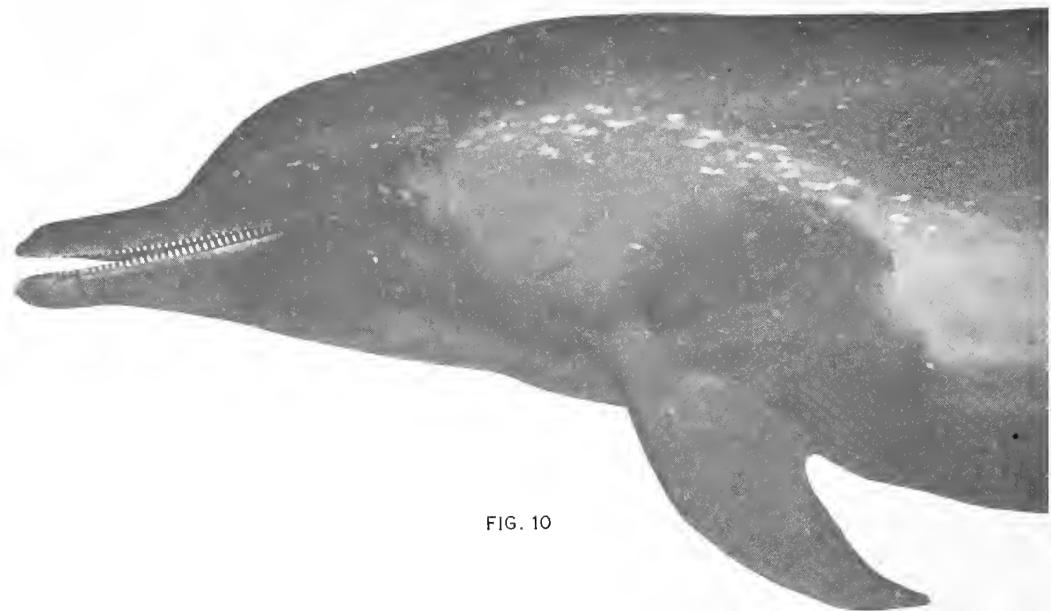


FIG. 10



FIG. 11

COLOR PATTERN OF THE EASTERN PACIFIC SPOTTED PORPOISE
STENELLA GRAFFMANI LONNBERG (CETACEA, DELPHINIDAE)



FIG. 12

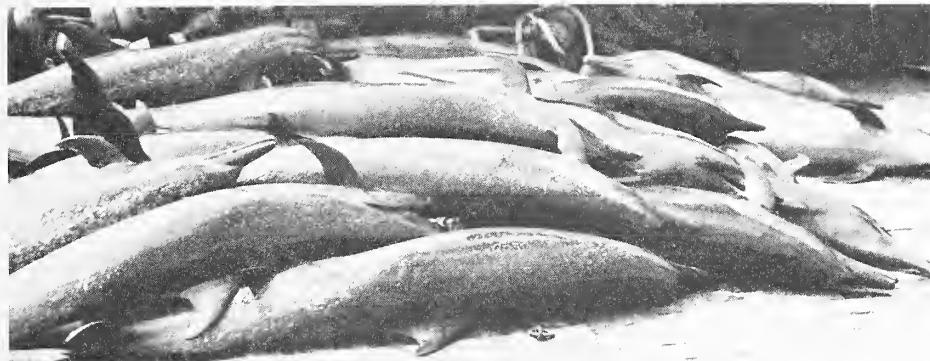


FIG. 13

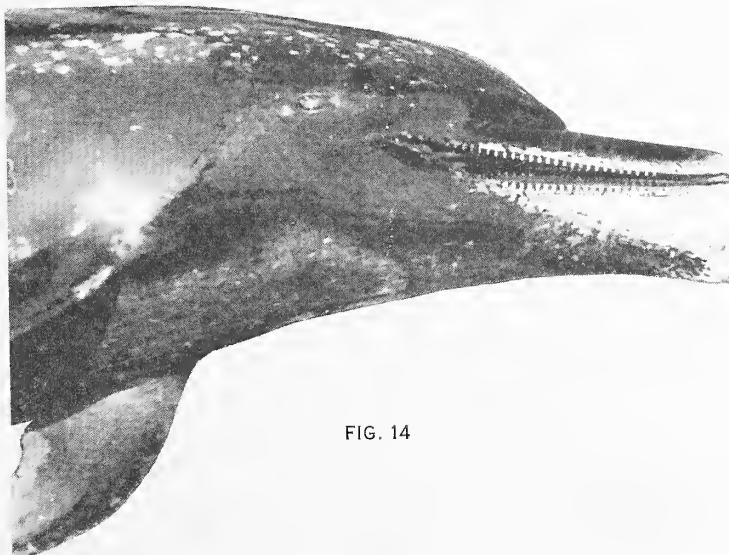


FIG. 14

COLOR PATTERN OF THE EASTERN PACIFIC SPOTTED PORPOISE
STENELLA GRAFFMANI LONNBERG (CETACEA, DELPHINIDAE)

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